W.P. Hiern Esq

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With the Author's Compliments.

THE

GENUS DIOSPYROS IN CEYLON: ITS MORPHOLOGY, ANATOMY, AND TAXONOMY.

PART I.

BY HERBERT WRIGHT.

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The Genus Diospyros in Ceylon: its Morphology, Anatomy, and Taxonomy.

BY

HERBERT WRIGHT.

Part I.

THE original portion of this paper deals exclusively with the genus Diospyros, *L.*, as represented in Ceylon by some twenty species, of which Trimen remarks: "Very little is known about many of our species, which are rare or local in the forests of the wet region and seem to flower but seldom. The native Sinhalese names are vaguely applied or very local, and refer more to the wood than to the trees themselves; and one is rarely able to obtain both wood and herbarium specimens from the same tree, in which way alone it is possible to be justified in definitely deciding the source of the former. The various rare mottled cabinet-woods, which appear to be produced only by very old trees, and are known as calamander (kalu-mediriya, wal-mediriya, ho-mediriya, &c.), have mostly yet to be referred to their respective species." In view of this lack of definite knowledge and the commercial value of ebony, calamander, and other timbers, the present investigation, which has occupied much time during the last three years, both in the forests and in the laboratory, was undertaken.

The present contribution is divided into two parts, the first part containing a general statement of, and a discussion on, the various subjects investigated; the second part a detailed

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description of each species. In Part I. the following arrangement has been adopted :—

I.—History. pp. 2 – 11.
II.—Distribution in Ceylon. pp. 11 – 14.
III.—Vegetative Characters. pp. 14 – 21.
IV.—Anatomy; Timber Properties, &c. pp. 21 – 55.
V.—Seedlings. pp. 55 – 67.
VI.—Reproductive Organs. pp. 67 – 105.
VII.—Affinity. pp. 105, 106.

I.—HISTORY. pp. 2 – 11.

Diospyros is the largest and most important genus of the Ebenaceæ, and since most papers dealing with this order contain a description of many of our species, it is necessary to trace the history of the literature on the whole subject to gain a better grasp of the general bearing of the particular species with which we are concerned.

The accumulation of knowledge regarding the Ebenaceæ has not been rapid, probably on account of the difficulty of obtaining representative material of a natural order so widely spread, and also in virtue of the comparatively unattractive nature of this group of plants. Though in 1753 Linnæus published the names of a few species, no work of a representative kind was published until that of Hiern in 1873. During that interval the work consisted mainly of collecting and describing species, remarking on fossil forms and affinities, and discussing the ebony yielded by this group of plants.

It was not until the latter part of the nineteenth century that any internal characters were used for systematic purposes, but since that time the majority of contributions have dealt extensively with the internal or microscopical construction of the vegetative parts. The only lines of study which have hitherto been neglected are those connected with the development and anatomy of the embryos and seedlings.

In 1753 Linnæus* described five species of the Ebenaceæ, two of which belonged to the genus Diospyros. New species and genera were subsequently described by Linnæus,† C. Linnæus,‡ and Loureiro,§ and others were figured and described by Roxburgh‖ and König in 1795. It was not until 1799 that the natural order Ebenaceæ was established by Ventenat;¶ subsequently it received considerable attention, many species and genera being quickly added from Mauritius by Poiret,** from Australia by Brown,†† from Java by Blume, from India by Wallich,‡‡ and from the Philippines by Blanco.§§

The Ebenaceæ of Ventenat, revised by Jussieu,‖‖ had by this time greatly enlarged, and the necessity for a further revision was obvious; accordingly, G. Don¶¶ undertook this work and gave a description of every species known to him.

This was speedily followed by more collecting, and finally A. de Candolle*** wrote a monograph on the whole of the Ebenaceæ. Having formed some definite ideas as to the external morphology of the Ebenaceæ, many botanists of that period turned their attention to the possible affinities of the order, and in 1845 we have the first fossil species described by Braun, and subsequent contributions on fossil species by Unger, Ettingshausen, Zollinger, and others.

The phylogeny of the order was discussed by Miers††† and Choisy,‡‡‡ the former proposing that the Ebenaceæ be

* Linnæus, Species Plantarum, 1753.
† Linnæus, 13th Edition of Systema, 1774.
‡ C. Linnæus in Supp. Spec. Plt., 1781.
§ Loureiro, Flora Cochinchinensis, 1790.
‖ Roxburgh, Coromandel Plants, 1795–1819.
¶ Ventenat, Tableau du Regne Végétal, 1799.
** Poiret, Encyclopédie méthodique, 1804.
†† Brown, Prodomus floræ novæ Hollandiæ, 1810.
‡‡ Wallich, East Indian Plants, 1828, 32.
§§ Blanco, Flora de Filipinos, 1837.
‖‖ Jussieu, Ann. du Museum, Vol. V., 1804.
¶¶ G. Don, General System of Gardening and Botany, Vol. IV., 1837.
*** Alph. de Candolle, Prodr. Syst. Nat. Regni Veget., Vol. VIII., 1844.
††† Miers, Contributions to Botany, Vol. I., p. 24, 1851.
‡‡‡ Choisy, Memoires des Ternstrœmiaceæ, p. 9, 1855.

regarded as a polypetalous group allied to the Anonaceæ, and the latter contending that they showed strong affinities to the Ternstrœmiaceæ.

The technical value of the timber had also gained a high reputation, and many botanists discussed the origin of the term "ebony," Bertolini* contending that the ebony of the ancients was not furnished by the Ebenaceæ.

From the time of publication of the monograph by A. de Candolle in 1844 up to 1873 no work of great systematic importance was produced. In the meantime several species had been described or figured by Wight (1850), Dalzell (1852), Martins and Miguel (1856), Thwaites (1854–64), Beddome and Kurz (1871), Mueller and Bentham (1864–9), Oliver (1868–77), Eichler (1870–80), Bentham and Hooker (1872–3), and Grisebach in 1872. These, together with short accounts of the fossils, affinity, and the timbers, were all that appeared in the thirty years subsequent to the monograph by A. de Candolle.

In 1873, however, Hiern† published his monograph, which is without question the most comprehensive work on the subject. This work is purely systematic, and deals with the characters of the floral and vegetative members, the distribution of the species, their probable affinity, and the several uses to which the parts of certain species are put. Hiern distinguishes five genera, two being endemic in Africa (Royena and Euclea), one (Tetraclis) in Madagascar, and the others (Maba and Diospyros) represented in many parts of the world. The genus Diospyros, as described by Hiern, contains 160 species, and is therefore by far the most important in the order. With it Hiern has united the genera Cargillia, *R. Br.;* Leucoxylum, *Blume;* Noltia, *Schum.;* and Gunisanthus and Rospidios, *DC.* The second largest genus—Maba—includes Macreightia, *A. DC.*, and Rhipidostigma, *Dalz.* The three remaining genera contain a total of

* Bertolini, Miscellanea Botanica, XII., 1849.

† W. P. Hiern, A Monograph of Ebenaceæ, Trans. Camb. Phil. Soc. Cambridge, 1873.

thirty-three species, and since they are not represented in the flora of Ceylon, they need not be considered here.

The Brazilian genus Brachynema, *Benth.*, and the Javanese Drebbelia, *Zoll.*, are regarded by Hiern and others as being non-Ebenaceous, and as probably of Olacinaceous affinity.

The five genera recognized by Hiern are so closely associated with one another that many botanists have suggested the advisability of uniting all into one genus.

Hiern bases his classification of the genera mainly on the sex of the flowers, having the genus Royena with hermaphrodite or rarely subdiœcious flowers; the remaining genera, including Diospyros, with diœcious or rarely polygamous flowers. The observations were made upon material from the recognized herbaria of Europe, and a small quantity of spirit material obtained from Dr. Thwaites, Ceylon.

As will be shown later, the sex of the Ceylon species of Diospyros has been imperfectly and often erroneously described as a consequence of examining only herbarium specimens instead of the fresh material in the jungle.

The effect of Hiern's admirable monograph is well seen if one considers the history of the development of our knowledge prior and subsequent to its publication. Since 1873 but little has been contributed to our systematic knowledge of the Ebenaceæ, and from that time the anatomists have been at work on the basis laid down in Hiern's monograph. Their investigations have resulted in more definite knowledge regarding the structure of the leaves, the secondary tissues of the stem, and the nature of the causes leading to the discolouration of the timbers.

Wiesner* described the internal characters of the stems of some Ceylon species of Diospyros, and gave details of an onerous method of preparing sections of ebony, which was subsequently adopted by Molisch. His work was succeeded by contributions from Moeller,† in which the anatomy of

* Wiesner, Ebenholz, 1870.

† Moeller, Holzanat., in Denkschr. Wiener Akad., 1870–3.

the axis was more thoroughly dealt with, and a theory was set forth explaining the enhanced durability of ebony as a consequence of the walls of the elements being impregnated with a colouring substance of unknown chemical constitution.

A much more instructive paper was then issued by Molisch,* who prepared his sections by the method of Wiesner. Molisch described the anatomy of the stem of two of our species, D. Ebenum, *Koen.*, and D. sylvatica, *Roxb.*, together with three others, and a species from each of the genera Maba, Euclea, and Royena. He attempted to combine the facts of internal construction with external morphology, believing with Radlkofer that this would provide the best basis for a systematic grouping of the plants. He also laid stress on the striking anatomical resemblances of the species he examined, and endeavoured to discover whether the reason of the high technical value of the ebony woods lay in the anatomical construction or in the chemical changes going on within the tissues.

In connection with the colouring matter of the timbers, he believed that the initial deposits were true gums, and that the suspected resin was a product of a slow process of humification going on within the elements. He further endeavoured to show that seasonal rings of growth were found in the secondary xylem of trees of D. Virginiana, *L.*, which had been grown in Europe, whereas those grown in the tropics showed no such histological differentiation. The various points raised by Molisch will be subsequently discussed under their respective sections in the present contribution.

Hartig† has given an account of the timber of several species, and has discussed the views of Moeller and Molisch as to the nature of the colouring substance in ebony. He

* H. Molisch, Vergleichende Anat. des Holzes der Ebenaceen und ihrer Verwandten. Sitz. Akad. Wiss. zu Wien, Bd. 80, Abth. 1, 1879.

† Hartig, Bot. Ztg., p. 108, 1859, and also Lehrbuch für Förster, I. Theil, p. 256, 1861.

believed that the coloured body filling the lumina of the secondary xylem elements was neither a gum nor a resin, but one of unknown and singular chemical composition. This subject was then taken up by Belohonbek* and Höhnel,† the former concluding, after a detailed chemical analysis, that the black contents of the timber, soluble in alkali, were mainly humus acids, and the remaining material, insoluble in alkali, more or less pure carbon.

Moeller made another contribution at about the same time dealing with the anatomy of the bark, and the origin layer of the phellogen. Solereder‡ also made additions to our knowledge on the same subject, and described the histological details of the secondary elements and the papillæ on the under surface of the leaves of many species. Radlkofer§ discussed the value of internal characters, and stated that in the Ebenaceæ the affinity so apparent in the flowers may be reflected in the anatomical construction of the vegetative parts. In the same year Weiss‖ and Gürke¶ published works on the Ebenaceæ; the former dealing with the nature and origin layer of the phellogen and its products, and the latter discussing the leading anatomical and morphological characters as known to him.

In 1892 the last anatomical contributions to our knowledge of the Ebenaceæ were made by Pomrencke** and Parmentier,†† the former dealing comparatively with the timbers, and the latter giving a detailed account of the anatomy of the vegetative members of very many species. The contribution

* Belohonbek, Ebenholz, in Sitzb. K. böhm. Gesellsch. d. Wiss in Prag., 1883.

† Höhnel, Stockwerkart Holzk., in Sitzb. Wiener Akad., Bd. LXXXIX., Abs. 1, p. 42, 1884.

‡ Solereder, Holzstruktur, 1885, pp. 68–169.

§ Radlkofer, Durchs. P. in Sitzb., Münch. Akad., 1886, p. 323.

‖ Weiss, Korkbild., in Denkschr. Regensb. bot. Gesellsch., 1890, p. 57.

¶ Gürke, in Nat. Pfl., IV. Theil, Abth. 1, 1890.

** Pomrencke, Holz. einig. symp. Fam. in Arb. bot. Gart. Breslau, 1892, p. 49–51.

†† Parmentier, Histologie comparée des Ébénacées, Paris, 1892. 155 figs., 4 pls.

by Parmentier contains a general discussion of the anatomical and morphological characters of the genera, and a detailed description of the anatomy of the leaves of seventy species of Diospyros and of other fifty species belonging to the remaining genera. Several complicated and ingenious tables are given, intended to show the relationships of the species of each genus to one another, the conclusions being based on the work of Hiern and the anatomists previously mentioned. Analytical tables for the genera and species are constructed on the sex characters of the flowers as determined by Hiern, together with the pericyclic or sub-epidermal origin of the phellogen in the stem. Parmentier believes that the genus Diospyros is characterized by a sub-epidermal phellogen in the stem, and on this ground, since D. oppositifolia, *Thw.*, and D. suberifolia, *Dcne.*, have a pericyclic phellogen, he transfers them to the genus Euclea.

Such a position is untenable, and it is unwise to lay down such rigid classifications from observations on only 40 per cent. of the species of Diospyros; furthermore, the sex of one of the species, viz., D. oppositifolia, *Thw.*, was not then known, and though it was regarded as being diœcious, I have since been able to prove that it is monœcious only. The classification put forward is further weakened by the discoveries regarding the true nature of the sex of Diospyros, and the behaviour of the phellogen in the pericycle and cortex of the primary axis.

The detailed accounts of the parts of the leaf and the grouping of species of Diospyros according to the subcentric or bifacial mesophyll, the immersion or projection of the median and lateral traces, and similar leading characters are particularly instructive, though we cannot but regard the tables of affinity, such as that on pages 56–57, as being premature, seeing that our knowledge of the whole order was then, and still is, meagre and unreliable.

We have seen that from 1873 the main work has been on the anatomy of the stem and leaves and the origin layer of

the phellogen. Smaller papers appeared during that period from Hiern* on new species and from Naudin† on the general natural history of the cultivated forms. Contributions of systematic significance were issued by Kurz‡ and Vesque,§ the latter working on the lines of Parmentier and pointing out many epidermal characters of specific importance.

The timbers also received the attention of Brandis,‖ and in more recent times were studied by Broun¶ and Ursprung.** The last-named botanist has compiled some very instructive information regarding the seasonal histological differentiation in the secondary xylem of tropical grown trees, including several Ceylon Diospyros species.

There has been only one publication dealing extensively with the Ebenaceæ during the present century, this being a purely systematic work by Hallier†† in 1901. Hallier deals with the relationships of the Tubifloræ and the Ebenales in a very general way, and from considerations upon the morphology of the flowers, fruits, and seeds, together with the phyllotaxis of the members concerned, he builds up a complicated table intended to show the polyphyletic origin of the sympetalous and apetalous flowering plants. He contends that the Ebenales show a close relationship with the Anonaceæ, Scytopetalum, Geraniaceæ, Dipterocarpaceæ, Sapotaceæ, and makes suggestive remarks as to their possible affinity to the Ancistrocladeæ, Convolvulaceæ, Quinaceæ, and many other natural orders. The contribution is full of

* Hiern, notes on Ebenaceæ, Jour. of Bot., XII., XIII., XV., 1874, 75, 77.

† Naudin, Quelques remarques au sujet des Plaqueminiers cultivés à l'air libre dans les jardins de l'Europe ; in Nouv. archiv. du Mus. d'hist. nat.. Paris, 1880.

‡ Kurz, Flora of British Burma, 1874–7.

§ Vesque, Gamopétales in Ann. Sc. nat., Ser. 7, 1885.

‖ Sir D. Brandis, Conf. Ind. Timbers, Col. Exh., 1886.

¶ A. F. Broun, Ceylon Ebony, Indian Forester, July, 1899.

** A. Ursprung, Beiträge zur Anatomie und Jahresringbildung tropischer Holzarten ; Inaug. Disser. Hohen. Phil. Fac. ; Basel, 1900.

†† Hallier, Uber die Verwandtschaftsverhältnisse der Tubifloren und Ebenalen, den polyphyletischen Ursprung der Sympetalen und Apetalen und die Anordnung der Angiospermen überhaupt. Hamburg, 1901.

interesting suggestions, and convinces one that there is no finality in pointing out the morphological resemblances between widely separated families. There is no difficulty in tracing a particular character of a floral or vegetative member through numerous non-related natural orders; in some orders the character is presented in a suppressed or enhanced form, and to deduce affinity therefrom inevitably leads to a confused notion as to the true significance of the feature dealt with.

The subject, as dealt with by Hallier, is very complicated, and in the end one gains very little precise information as to the phylogeny of any group of Angiosperms with which he has dealt.

Local History.—In connection with the history of our knowledge of Ceylon species, twenty in number, there are several interesting facts to record.

Though some of the species of Diospyros occurring in Ceylon are to be found in Malaya, Burma, Tropical Australia, Peninsular India, Anamalai hills, Tinnevelly, and South India generally, there are several endemic forms.

D. Ebenum, *Koenig*,* was the first species found in Ceylon, in 1776, but it has since been discovered in many parts of Southern India and in Malaya. It is the chief source of ebony in Ceylon, and the high commercial value of the timber was probably the reason of its being the first species to be recognized. It was not until five years later that the next species was discovered, D. hirsuta, *L.*,† an endemic form very common in the wet low-country.

In 1795 Roxburgh‡ discovered on the Coromandel Coast three species which were subsequently found wild in this Island, viz., D. Melanoxylon, *Roxb.*, the source of most of the Indian ebony, but nearly extinct in Ceylon; D. montana, *Roxb.*, a species abundant in the low forests of the

* Koenig, in Phys. Salsk. Handl., Vol. I., p. 176, 1776.

† Linnæus, Suppl. Plant., p. 440, 1871.

‡ Dr. Roxburgh, Coromandel Plants, Vol. I., pp. 36, 37, 38, t. 46, 48, 47, 1795.

hot dry country in Ceylon; and D. sylvatica, *Roxb.*, now only rarely met with in this Island. In 1807 D. Embryopteris, *Pers.*,* and in 1827 D. Toposia, *Ham.*,† were found, the former first in the East Indies and the latter in Bengal, but both subsequently found in very many parts of Ceylon. Nearly a quarter of a century passed before the next Ceylon species was found, and this discovery—D. ovalifolia, *Wight*‡—was first made in Madras. This was speedily followed by the discovery of D. pruriens, *Dalz.*,§ first in Bombay by Dalzell, and subsequently in the Sabaragamuwa Province by Thwaites.‖ By that time Dr. Thwaites, then Director of the Royal Botanic Gardens, Peradeniya, had commenced the work of collecting the plants of Ceylon, and his discovery of D. pruriens, *Dalz.*, in Ceylon, so soon after that by Dalzell, was followed by the discovery of ten¶ species of Diospyros in 1860; seven of these have not yet been found out of Ceylon, and some of them are at the present time exceedingly rare. The species found were:—D. crumenata, D. affinis, D. quæsita, D. oocarpa, D. insignis, D. oppositifolia, D. Gardneri, D. Moonii, D. acuta, and D. attenuata. Since then only one species has been added to the Ceylon group, viz., D. Thwaitesii, by Beddome** in 1871, a form peculiar to this Island.

Locally, no further original work has been done on the genus Diospyros other than what is represented in Dr. Trimen's "Handbook of the Flora of Ceylon."

II.—DISTRIBUTION IN CEYLON.

The forest vegetation in Ceylon varies according to the rainfall and elevation, and as far as the genus Diospyros is concerned we may speak of the species as being dry, wet,

* C. H. Persoon, Synopsis Plantarum, Vol. II., p. 624, 1807.
† Hamilton, Trans. Linn. Soc., Lond., Vol. XV., p. 115, 1827.
‡ Dr. Wight, Icones Plant. Ind. Orient., t. 1,227, 1850.
§ Dalzell, Kew Journal of Botany, Vol. IV., p. 110, 1852.
‖ Trimen, Flora of Ceylon, Vol. III., p. 95.
¶ Thwaites, Enum. Plant. Zeyl., pp. 179-182, 1860.
** Beddome, Ic. Pl. Ind. Or., p. 27, t. cxxxv., 1871.

or intermediate zone plants. In the dry zone, where the rainfall ranges from 35 to 70 inches, we have seven species, viz., D. Ebenum, D. Embryopteris, D. Melanoxylon, D. oocarpa, D. montana, D. affinis, and D. ovalifolia. The majority of these species, particularly D. Ebenum, D. ovalifolia, and D. Embryopteris, are to be found in abundance in local areas of the dry zone. D. oocarpa is less common, though at Mihintale, Dambulla, Haragama, Maturata, and Kalugala it is abundant in many of the forests. Of the dry zone species D. Melanoxylon has the most limited distribution. It was first found by Dr. Trimen* between Bibile and Ekiriyankumbura in 1888, and the fact that its existence was not determined by Dr. Thwaites is sufficient to show its rarity. In 1901 its presence was again noted in this locality, and in addition a large number of plants were found on the patana and in the coarse forests at Elukapudena and Diggalrana to the south-west of Bibile. Many large trees were also found along the roadside from Bibile to Bintenna, and in the forest along the side and at the base of Bibile hill.

The remaining thirteen species occur in the wet zones, where the rainfall is never less than 80 inches, and in places often reaches over 300 inches per annum, and at elevations from sea level to 4,000 feet. The most generally distributed species are D. insignis and D. Toposia. In the districts around Ratnapura, Sinha Raja forest, Pasdun korale, and Hiniduma, the species D. hirsuta, D. Moonii, and Thwaitesii are specially abundant. In the higher parts of the wet zones, as at Ambalawa, Hantane, Kadugannawa, and Gangaruwa, abundance of D. crumenata, D. Gardneri, and D. sylvatica is met with. The remaining species are rare, and occur in the low-lying wet forests of the Southern and Western Provinces.

The rarest of the wet zone species is undoubtedly D. oppositifolia. Specimens of this species were collected at Hiniduma in 1853 by Dr. Thwaites, and this was the only material which Dr. Trimen ever saw. This species is

* Flora of Ceylon, Vol. III., p. 99.

limited to the upper part of Hinidunkanda, a hill in the Southern Province some 2,200 feet high. The upper part of this hill is for the greater part of the year enveloped in clouds, and it is only between 1,500 and 2,000 feet that this species occurs. It is particularly abundant, together with D. quæsita, on the north-west flank, and is entirely absent from the eastern part of the hill. The species D. acuta and D. attenuata are the next in point of rarity, they being limited to the low wet country between Hinidunkanda and Pitigala. Both species occur in abundance in the damp forests of Wewella, Pasdun korale, and D. acuta extends to the Wirakanda forests near Hewessa.

The remaining wet zone species—D. pruriens and D. quæsita—occur in the wet forests of Karawita, Sinha Raja, Hiniduma, and Yagirala. D. pruriens reaches its maximum dimensions and is most abundant in the forests of the Adam's Peak Wilderness, and thrives best on the rocky soils in the vicinity of Magala, Kadawatta, and Eratna, where the rainfall is very heavy.

In the intermediate zones, where the rainfall varies from 70 to 80 inches, the whole of the dry zone species, excepting D. Melanoxylon, occur, but of the wet zone species, however, only two—D. Gardneri and D. sylvatica—occur.

Intermingling of Dry and Wet Zone Species.

One rarely meets with any of the thirteen species of the wet zone in a purely dry zone. D. Moonii, a species possessing relatively thick fleshy leaves, is reported from dry places along the coast, though it is most characteristic of districts where the rainfall is great. Again, D. insignis, a species generally distributed in the wet zone, occurs in the Pindeniya and Kegalla districts. None of the wet zone species have ever been reported from the arid zones of the Island.

On the other hand, at least two of the dry zone species—D. Ebenum and D. Embryopteris—constantly recur in

truly wet zones. These two species, though attaining their maximum distribution in the dry areas around Anuradhapura, Trincomalee, Vavuniya, &c., may also be found in the low-lying forests of Sabaragamuwa and the Central Province. sometimes being very plentiful along the banks of streams. In the moist regions D. Ebenum may extend up to 4,000 feet, many occurring at Hantane, Ambalawa, Gangaruwa, Hinidunkanda, Borulugoda, Eratna, and Hewessa. The dimensions of trees of these two species when in the wet zone are usually but not always less than those from a dry zone. Specimens of D. montana, D. oocarpa, D. ovalifolia, or D. affinis have not yet been recorded from any wet zone area, though D. oocarpa is known in the intermediate zone.

III.—VEGETATIVE CHARACTERS.

Dimensions, Habit, &c.—As far as the Ceylon representatives of the genus Diospyros are concerned, every species assumes an arborescent habit.

It is characteristic of the dry zone species to attain huge dimensions. D. Ebenum, being the main source of ebony in the Island, is usually felled after attaining a breast-height circumference of 6 feet, but further increments are possible, and many trees are known with a circumference of 9 to 10 feet. Specimens of D. affinis in the Viriniya and Bibile districts and of D. Embryopteris at Anuradhapura often attain a circumference of 9 feet and possess an unbranched bole over 50 feet in length. The total height of the dry zone species is often over 100 feet, and the huge dimensions are only departed from when the plant occurs in the wet zone areas.

There is, however, one district in the wet zone where trees of D. Ebenum and D. Embryopteris attain dimensions which outrival those known in the dry zones. I refer to the Ambalawa district on the boundary between the Central and Sabaragamuwa Provinces, where the rainfall is over 100 inches a year and the elevation varies from 2,000 to 3,500

feet. Here there is one specimen of D. Embryopteris measuring no less than 16½ feet in circumference, not allowing for the undulations in outline, which, if taken into account, would give a total circumference of over 20 feet and a height of 130 feet. Specimens of D. Ebenum also occur in the same forest which have a circumference of nearly 13 feet and a total height of 100 feet.

With the wet zone species there is likewise a wide range of variability, though only few species attain the huge dimensions of the dry zone plants.

Among the smallest trees we may place D. pruriens, since in the Sinha Raja district a single plant is often of convenient size for a herbarium sheet. This species, when it attains its maximum dimensions along the rocky slopes of the Peak Wilderness, rarely exceeds a total height of 9 metres (30 feet) and a circumference of 30·5 cm. (12 inches).

In point of size, D. acuta and D. attenuata come next to D. pruriens. In the wet forests of Pasdun korale these species occur in the form of small trees, from 20 to 30 feet in height and 1 to 4 inches in diameter. The leaders have often a weeping habit, particularly in D. attenuata, and though only 1 inch in diameter, may bear abundance of flowers and fruits. One specimen of D. attenuata was obtained in flower in the Wewella forest which had a short straggling leader only 14·0 cm. in diameter. Trees of these species frequently occur in groups of three to fourteen trunks matted together by dense woody roots at the common base of the trunks, and this, together with the weeping habit, is suggestive of the bamboo clumps growing in the same area.

D. hirsuta, though occurring so abundantly along the streams around Ratnapura, Eratna, and Hiniduma, rarely exceeds 9 metres (30 feet) in height and 20 cm. (8 inches) in diameter. When the stem is only 7·5 to 10·2 cm. (3 to 4 inches) in diameter the plant bears fertile seeds.

D. Thwaitesii, except in the Hiniduma district, is a tree similar in size to D. hirsuta, and in the Hewessa and Palakete

forests rarely exceeds a total height of 30 feet and a diameter of 5 inches. In the Hiniduma district, however, particularly along the north-west side at an elevation of 1,000 feet, many specimens of D. Thwaitesii attain a total height of 15·2 to 18·3 metres (50 to 60 feet) and a breast-height circumference of 50 to 76 cm. (20 to 30 inches).

D. insignis, characterized by its straight leader unbranched to a height of 6·1 metres (20 feet), is likewise of comparatively small dimensions. The breast-height circumference rarely exceeds 64 cm. (25 inches), and many plants having a main stem less than 12·7 cm. (5 inches) diameter bear a considerable amount of fruit.

The above-mentioned species may be regarded as those in the wet zone, which are characteristically of small dimensions. Commencing with the class possessing species of relatively large dimensions, we may for the sake of a continuous series first consider the smaller members, D. Moonii and D. oppositifolia, which thrive best along the banks of streams or along damp precipitous slopes, and usually attain a total height of 12·2 to 18·3 metres (40 to 60 feet) and a breast-height circumference of 610 to 915 mm. (2 to 5 feet). Nevertheless, specimens of D. Moonii in the Hewessa district and D. oppositifolia on the western side of Hinidunkanda occur as clumps of thin leaders matted together at the base by a common system of roots.

Next to these we may place D. quæsita, D. Toposia, and D. Gardneri, since they often attain a total height of 30·5 metres (100 feet), and many exceed a breast-height girth of 1·8 metres (6 feet).

The remaining wet zone species, D. crumenata and D. sylvatica, may attain dimensions which rival the colossal species of the dry zone. The largest specimen of D. sylvatica in Ceylon is probably at Ambalawa, near Gampola, since it consists of a main stem 4·2 metres (13½ feet) in circumference which remains unbranched for a distance of 24·4 metres (80 feet). At this height the stem branches, one fork then

continuing its upward course through a distance of over 30·5 metres (100 feet). In the Ambalawa and Dambalagalla districts there are some very fine patches of forest in which trees of Diospyros species are very abundant and attain huge dimensions.

Branch System.—The branch system is invariably well developed. Though the conditions of canopy do to a very great extent determine whether the branches shall grow erect, horizontal, or assume a weeping habit, yet it seems characteristic of certain species to possess branch systems of a fixed type. For instance, under conditions of open or close canopy, *i.e.*, either exposed equally on all sides or in dense forest, trees of D. Embryopteris have a branch system usually nearly horizontal. Again, D. quæsita has a branch system spreading at an angle of 40° to 50,° and according to Hiern the branch system of D. sylvatica spreads at 60° to 70°. Specimens of D. attenuata growing in dense forest have invariably a weeping habit, though the weight of foliage, &c., is never great.

Phyllotaxy.—In the majority of the Ceylon species the alternate arrangement of the leaves is characteristic on twigs of the mature plant. Small shoots of D. Moonii have often large leaves arranged alternately along the length of the thin stem. The final disposition of the mature leaves is usually one which ensures the maximum of light on their upper surfaces, and many leaves in their attempts to attain this position have undergone much twisting, particularly in the region of the petiole. There are, however, three of our species in which the phyllotaxy departs from the alternate type.

The leaves of D. Melanoxylon are usually opposite; sometimes they are sub-opposite and occasionally alternate. In very many instances the leaves are densely crowded, either at the end of a twig or near the main stem. D. insignis has the majority of its leaves disposed alternately

and the remainder sub-opposite. D. oppositifolia resembles D. Melanoxylon in the opposite and sub-opposite arrangement of the leaves. In the former species, however, many twigs have their leaves crowded together to form large rosettes.

Form and Size of Leaves.—The leaves conform to the usual tropical type in that they are simple, entire, and petiolate. The shape may be ovate (D. ovalifolia), lanceolate (D. hirsuta), or lanceolate oblong, with a tapering or abrupt apex, and a rounded or tapering base.

The size varies considerably, being smallest (30 to 70 mm.) in D. oocarpa and D. pruriens, and largest (190 to 350 mm. long) in D. Moonii, D. insignis, and D. Embryopteris. Within the same species there is often a considerable variation in size, the young leaves arising on offshoots from the main stem being many times the size of those occurring on the normal twigs. A case in point is in the large leaves of D. Melanoxylon, these occurring on the young shoots arising from the base of small trees and measuring 100 to 240 mm., whereas the normal dimensions for this species are 50 to 100 mm. Heterophylly occurs to a marked degree in D. Gardneri, D. oppositifolia, and D. sylvatica.

Venation.—The vascular bundles in the leaf form a central stout midrib with several smaller lateral factors connected alternately along its length, these in their turn being made up by the coalescence of the very small bundles scattered between them. Sometimes the vascular bundles project strongly on the upper surface (D. Embryopteris), sometimes on the lower surface (D. insignis), but are often relatively inconspicuous (D. affinis, D. montana, and D. oocarpa).

The midrib may be very conspicuous, as in D. Moonii and D. acuta, or it may be insignificant as in D. oocarpa and D. attenuata.

The lateral and reticulate bundles are invariably pellucid; sometimes this character is not very conspicuous, as in D. affinis; in other species, particularly D. Embryopteris, D. Ebenum, and D. Toposia, the translucent character of the small bundles is the most striking feature of the foliage.

The reticulate meshwork is of a closely knit nature in D. Toposia; and in D. Embryopteris, particularly var. nervosa, the meshwork is wide.

The pellucid venation, though characteristic of every Ceylon species of Diospyros, is not limited to this group of plants. It is prominent throughout the Anonaceæ, and also characterizes the foliage in species of Anacardium.

Climatic Types.—The majority of the Ceylon species have tough coriaceous leaves, this being particularly characteristic of D. insignis, D. Embryopteris, and D. Ebenum. The coriaceous type of leaf is prevalent in nearly every one of our dry zone species. In the wet zone species we may have the fleshy type of leaf, as in D. acuta and D. Moonii; the densely pubescent and thin type, as in D. pruriens; or the normal tender leaves, as in D. attenuata and D. Thwaitesii. The fleshy type and the densely pubescent type are, as far as the Ceylon species of Diospyros are concerned, limited to the very wet zone. The pubescent type, as exemplified in the leaves of D. pruriens, is found in a part of the Island where the rainfall is never less than 300 inches per year; D. hirsuta, which in point of pubescence comes next to D. pruriens, likewise thrives best in the wet districts of Eratna and Ratnapura.

Persistence of Foliage.—The Ceylon species of Diospyros are of the evergreen type. This is characteristic of the genus throughout the world, there being very few exceptions, notably D. Tupru, *Buch.*, which according to Beddome sheds all its leaves in the cold season and produces new ones in the beginning of the hot weather. The twigs of D.

montana and D. ovalifolia become partially leafless every year in the dry northern districts of Ceylon.

In Ceylon the leaves of most species of Diospyros drop at irregular intervals, and if one tree be selected for observation there is hardly a week passes without a shedding of a few leaves. The leaf-fall in most species is not sufficient to render the tree even partially bare, and the nett result of the leaf production, which repeatedly occurs, is an increase of foliage from year to year. The production of new leaves takes place during nearly every month of the year, if one considers the whole of the Diospyros species in the Island. If, however, one selects a district where the force of each monsoon and the intervening lulls is felt, a regularity in the leaf production is noticeable.

In the Peradeniya district there is an annual production of leaf in flowering trees of D. Gardneri, D. Embryopteris, D. Ebenum, D. affinis, D. Toposia, D. sylvatica, and D. crumenata. In non-flowering trees of D. Embryopteris there is a production of new leaf twice yearly, this occurring during the months of April to June and October to November.

The production of new leaf on any particular tree may be completed within one month, or new foliage may appear for several months in succession. The prolonged period of active growth occurs in one tree of D. Toposia from December to June, and again in trees of D. Ebenum leaf production may commence in December and continue for four or five months. Other trees of D. Toposia and D. Ebenum in the same and also adjacent districts may not produce any new leaves until well on in the months of February and March.

Respecting other species of Diospyros, particularly D. hirsuta and D. Thwaitesii in the wet zone, I have never visited the forests without finding some trees in new leaf during nearly every month of the year.

In the wet zone it is impossible to speak of any month as being specially noticeable for leaf production within the

Diospyros genus. The leaf production is apparently not of such a nature as to severely tax the resources of the plant, and its occurrence is probably to be correlated with individual requirements rather than with climatic conditions.

This can only obtain in the vegetation of the tropics where the temperature and rainfall are relatively equable throughout the year.

IV.—ANATOMY, TIMBER, &c.

Stem.—In the genus Diospyros the phellogen is often said to be of sub-epidermal origin, and this is considered by Parmentier and Solereder to be of taxonomic importance, the former using this as one of the main characters in his proposed grouping of the genera. The phellogen, however, actually arises either immediately beneath the epidermis or from the pericycle, the latter origin being conspicuous in the primary axis or hypocotyl of the seedlings.

The sclerotic or stone cells of the cortex are conspicuous in D. Ebenum, and the various stages of their formation and degeneration are shown. (See pl. XIX., figs. 1–4); they are relatively short, thick walled, and well pitted; finally they lose their definite outline and form hyaline masses of tissue, which do not respond to the commoner staining reagents. In longitudinal section they are seen to be surrounded with parenchyma and long sclerenchymatous fibres. The phloëm and cambium are of the ordinary type, and we may proceed to deal with the anatomy of the secondary xylem.

The observations of Molisch, Möller, Solereder, and Parmentier, already referred to, all agree as to the regular composition of the secondary xylem, the scarcity of tracheids, and the distribution of the elements.

Molisch obtained his sections of the hard brittle ebony by the method of Wiesner, which is briefly as follows: A thin slip of ebony, 2 to 3 cm. square, is cut by a fret-saw and fastened by means of sealing wax to a cork; both sides of the section are then polished on a smooth rotating wheel,

and when sufficiently thin the section is removed and finally polished on a razor stone. This method allows one to obtain fairly large sections, though smaller sections cut by hand in the ordinary way provide ample material for obtaining all points in detail.

Histology of the Timbers.—The anatomy of the secondary xylem of the Ceylon species of Diospyros is of the ordinary arborescent dicotyledonous type. The differentiation of the tracheal elements and fibres is remarkably uniform, but the parenchymatous tissues exhibit sufficient variation to allow of a grouping of the various species under different types. In dealing with the distribution, size, form, and percentage number of the secondary xylem elements one must allow for variability even for members of the same species, since they may have developed under quite dissimilar climates and their internal requirements are probably at great variance. As far as possible the statements have been made in a general sense, and where it has been possible to obtain material of the same species in the dry, wet, and intermediate zones, this has been done.

Tracheal Elements.

The tracheal elements are almost wholly represented by vessels; tracheids are never abundant, and when present usually occur alongside a large vessel.

Vessels.—The distribution of these elements varies according to the species, the age of the secondary xylem, and the climatic conditions under which the plants have grown. Usually the vessels occur in a more grouped condition in the xylem of the first few years than in the sapwood of old trees.

In some species the heartwood appears to be characterized by an equal number of isolated vessels and radial groups of two or three cells. Usually the members of vessels, when occurring in groups, form rows two to four cells in radial thickness; in others, notably D. attenuata, the groups may contain twenty members arranged one to two cells in

tangential width. Sometimes one group is separated from its neighbour only by a single line of medullary ray cells; usually, however, there is a wide band of fibres and parenchyma between parallel rows of vessels.

There does not therefore appear to be much regularity in the distribution of the vessels in the secondary xylem, and one may find as many as eight radial groups in one field, while adjacent parts of the same section may not show a single vessel, though the field of view is 0·6 mm. in radius. Usually, in passing from within outwards the vessels become more widely separated, tend to be more as single members, and are considerably increased in size.

In the sapwood of D. Moonii the vessels are nearer to one another tangentially than in the heartwood, yet in other species the space between the vessels increases from within outwards.

They are usually surrounded with fibres or flanked with short wood parenchyma or medullary ray.

The size of the members is never very great. The transverse and longitudinal dimensions show a regular increase as one passes from the heartwood to the sapwood, and it may be taken for granted that the larger the dimensions of the trunk the larger will be the dimensions of the vessels in the youngest part of the sapwood. This regular increase occurs in all our species, and is probably correlated with the physiology of the plant, particularly the storing and conducting of water. This increase of dimensions in the products of the old cambium is not characteristic of all the secondary xylem elements, and with the vessels we have to note that the increase of dimensions is concomitant with a decrease in percentage number and a more complete isolation from like elements. The fact that there is in every case a decrease in the percentage number when there is the maximum amount of foliage, and therefore probably maximum transpiration, renders some increase in size absolutely necessary when the heartwood is blocked up with gum and resin.

Dimensions of Vessels.

[Tw. = twig ; Sw. = sapwood.]

	Diameter. mm.	Radial Diameter. mm.	Tangential Diameter. mm.	Length. mm.
D. Ebenum	Tw. 6	0·045	0·034	0·31
	Sw. 360	0·085	0·081	0·45
D. quæsita	Tw. 15	0·04	0·04	0·22
	Sw. 190	0·13	0·07	0·43
D. oocarpa	Tw. 23	0·027	0·025	0·23
	Sw. 255	0·07	0·06	0·42
D. affinis	Tw. 9	0·03	0·03	0·22
	Sw. 200	0·12	0·08	0·45
D. montana	Tw. 8	0·04	0·07	0·34
	Sw. 175	0·07	0·05	0·36
D. Embryopteris	Tw. 9	0·04	0·04	0·31
	Sw. 360	0·14	0·09	0·43
D. Moonii	Tw. 15	0·06	0·05	0·27
	Sw. 165	0·18	0·10	0·35
D. attenuata	Tw. 6	0·025	0·028	0·21
	Sw. 140	0·09	0·06	0·32
D. pruriens	Tw. 9	0·038	0·04	0·26
	Sw. 80	0·11	0·10	0·44
D. acuta	Tw. 7	0·034	0·028	0·31
	Sw. 60	0·10	0·09	0·50
D. hirsuta	Tw. 10	0·03	0·026	0·41
	Sw. 75	0·18	0·09	0·45
D. Thwaitesii	Tw. 11	0·027	0·02	0·30
	Sw. 203	0·14	0·09	0·42
D. crumenata	Tw. 20	0·05	0·04	0·27
	Sw. 210	0·16	0·10	0·54
D. sylvatica	Tw. 9	0·03	0·028	0·20
	Sw. 405	0·13	0·09	0·36
D. Gardneri	Tw. 14	0·05	0·045	0·30
	Sw. 170	0·09	0·06	0·46
D. oppositifolia	Tw. 11	0·03	0·026	0·32
	Sw. 170	0·14	0·09	0·4–0·6
D. Melanoxylon	Tw. 10	0·023	0·03	0·36
	Sw. 270	0·13	0·09	0·46
D. ovalifolia	Tw. 22	0·024	0·024	0·20
	Sw. 240	0·05	0·05	0·40
D. Toposia	Tw. 14	0·027	0·03	0·27
	Sw. 250	0·09	0·05	0·30
D. insignis	Tw. 12	0·03	0·034	0·21
	Sw. 185	0·11	0·073	0·42

The dimensions of the vessels in the heartwood vary to a slight extent ; in the first three or four years' wood the radial diameter varies from 0·024 to 0·05 mm., the tangential diameter from 0·024 to 0·06 mm., and the length from 0·20 to 0·35 mm.

In the sapwood of the whole of our species the variation in radial diameter is from 0·05 to 0·18 mm.. and the variation in

length of the members of the vessels from 0·30 to 0·54 mm. This constancy in size throughout the genus in Ceylon is one of the main characters of the timbers. When one considers the climatic differences between Mannar and Adam's Peak Wilderness, one is led to expect that there will be great differences in the size of the water storing and conducting tissues in the species growing at these places, but such differences are by no means pronounced.

There is very little variation in the form of the members of vessels. In the heartwood the small-lumined vessels are, when isolated, approximately spherical or crudely hexagonal in transverse outline, but as one passes to the sapwood the increase in dimensions is more in the radial than the tangential direction, and as a consequence a radially elongated element presents itself. When the members are grouped, however, the spherical or elongated outline is rarely met with, one or more sides become straight, and the tangential diameter of each member is usually considerably more than the radial.

The sides of each member are characterized by a straight vertical course, and the original transverse partitions are only slightly inclined to the horizontal.

The walls of the vessels vary in thickness from 0·002 to 0·0035 mm. They are usually very well pitted. They are composed mainly of lignin, which continues to respond to the safranin and fuchsin tests even when considerably discoloured, and the lumina partially filled with coloured materials.

The function is probably that of storing or even conducting water, but when once the lumina are filled with gum and resin this function must be taken up by the younger tracheal elements. The vessels do not undergo depletion of coloured contents, the infiltrating materials increasing from time to time until the vessels are completely blocked.

Tracheids.—There is not very much to be said about these elements. They are only very sparsely distributed, and in

transverse sections only differ from the vessels in being usually of smaller diameter. They are generally limited to the neighbourhood of large vessels, frequently flanking the tangential surface, but in D. Embryopteris they may occasionally be seen among fibres.

The transverse dimensions are often only a trifle in excess of the largest wood parenchyma cells, but in some instances they attain a radial diameter of 0·04 to 0·08 mm. In length they come next to the fibres and may attain 0·27 to 0·90 mm. When of great length the ends taper very strongly, and in such cases it is difficult to distinguish them from the more abundant fibres, and the term "fibre-tracheids" would be very appropriate. The commonly small and constant transverse dimensions of true fibres seems to differentiate them from tracheids, but otherwise it often becomes well nigh impossible to distinguish a short fibre from a narrow lumined, long tracheid.

Parenchymatous Elements.

This includes the wood parenchyma, fibres, and medullary rays of the secondary xylem. It is in the distribution of these elements that the maximum variation occurs, and even in our Ceylon species it is sufficient to allow of a grouping of the species into sections according to—

(1) Whether the medullary rays are one cell in tangential breadth.

(2) Whether the medullary rays are more than one cell in tangential breadth.

(3) The presence of special radial groups of parenchyma.

As with the tracheal elements, the general features of distribution, histology, and function may be subject to all manner of variation according to the internal and external forces at work.

The parenchymatous tissues compose the greater part of the secondary xylem and increase considerably with the age of the cambium. It is obvious that the value of the timber

is greatly due to the percentage composition of elements of the parenchyma type and the structure and form of these elements.

In the poorer timbers the wood parenchyma is usually of the thin walled, wide lumined type, and this alone is often responsible for the inferior quality, for no matter how thick and long the surrounding fibres may be, the soft bands of parenchyma, when present, lead to early cracking and decay.

Wood Parenchyma.—In transverse sections the presence of these elements is usually determined by the abundance of carbohydrate and mineral contents, together with their relatively thin walls and wide lumina. Often, however, they are not easily distinguishable, sometimes because their transverse dimensions are similar to those of the neighbouring cells, as in D. quæsita; sometimes on account of the proximity of adjacent medullary rays, and again because the surrounding fibres may not have undergone much lignification; the latter is often the case in the secondary xylem of young twigs. In some species they are always very conspicuous, either on account of their lumina being very large, or because adjacent medullary rays are separated by patches of fibre of considerable tangential width.

The difficulty of distinguishing these elements, however, is only when one is limited to transverse sections; the great length of these elements and their numerous contents serve to isolate them in any longitudinal section.

The distribution of these elements is somewhat complex, and is such that a continuous system of elements of the parenchyma type is established, together with frequent direct and indirect contact with the tracheal elements. The wood parenchyma cells are distributed as tangential bands, oblique bands, and around large tracheal elements. The tangential bands usually extend from one medullary ray to another, and their significance varies according to the width of this gap; the tangential bands between adjacent rays in xylem of

the same age are connected by the intervening parenchymatous medullary ray cell, and a fairly continuous circumferential circulation of food materials can therefore be effected through such elements. In a few cases, however, the tangential line of parenchyma only reaches half way from one ray, the terminal cell appearing in transverse section to be surrounded by unlike elements; it is conceivable that there may be some connection in the vertical course.

In the majority of our species the tangential lines of parenchyma are only one cell in radial thickness; in some species, notably D. affinis they are very often two, and are occasionally grouped in the middle of a patch of fibres. In some specimens of D. hirsuta the bands—two cells in radial thickness—often run together through a vertical distance of over 0·8 mm. These tangential bands of wood parenchyma are separated from one another radially by patches of fibres from 0·06 to 0·18 mm. in thickness. These elements are therefore in communication with like elements or those of the medullary ray by means of their radial surfaces, with fibres by their tangential surfaces, and with tracheal elements by any surface.

The oblique bands of wood parenchyma are obvious in many species, and it is very probable that if sufficient material were examined they would be found to occur in all species.

The components of these bands, instead of being arranged to form one line parallel to the circumference, are arranged in radial series, one slightly internal to the next, and thus result in what may be described as a terraced system of parenchyma. Adjacent cells are usually in contact with one another by a part of their radial surfaces, and the terracing is therefore very gradual. Such systems of parenchyma connect one medullary ray to the next, but it is obvious that they tend to bring into direct communication the successive tangential bands between the same medullary rays, and therefore to establish a more thorough communication between like elements in tissues of different ages.

In some specimens of D. montana from Trincomalee I observed that some oblique bands of wood parenchyma were connected at the outer end to the median cells of a tangential band of parenchyma, and within, to a medullary ray at a point opposite to another tangential line of parenchyma. By this means tangential bands of one zone can be connected, almost directly, with a band in an older zone, along a different radius. Such an arrangement must greatly facilitate the transference of food materials through the parenchymatous system.

The tangential and oblique bands of wood parenchyma therefore effect an excellent communication with all elements, excepting perhaps the vessels and tracheids. The remaining part of the wood parenchyma is, however, specially associated with these elements. In most of our species the large vessels are surrounded or flanked on their tangential surfaces with relatively wide lumined but short wood-parenchyma cells. These are in communication with the other cells of wood parenchyma or medullary rays, and therefore a complete communication is effected with every element of the secondary xylem.

The vertical distribution of these elements is easy to follow since they are arranged one above another through a considerable vertical distance. They form very long columns of cells, often as many as twelve cells in the same row. The majority form single straight lines with the components exactly above one another; frequently one cell abuts on to another, not end to end, but by the radial walls, thus giving the terraced system in the vertical direction.

There is nothing unusual in the form of these elements. In transverse outline they may be any shape from circular to crudely four-sided, but only rarely do they exhibit sharp corners. They are elongated considerably in the vertical direction, the vertical walls being straight and the end walls flat or occasionally tapering at one end when in contact

with unlike elements. When one end tapers the appearance is very similar to that of a short fibre.

There is a little variation in the transverse, but considerable in vertical dimensions throughout the species. In some species the relatively large transverse dimensions aid materially in distinguishing them in the wood of young twigs.

The following are the dimensions of these elements in the sapwood of the respective species :—

Species.	Radial Diameter. mm.	Length. mm.
D. Ebenum	0·015	0·03 to 0·12
D. quæsita	0·009	0·04 to 0·15
D. oocarpa	0·013	0·06 to 0·13
D. affinis	0·016	0·09
D. montana	0·02	0·07 to 0·20
D. Embryopteris	0·01	0·09 to 0·13
D. Moonii	0·015	0·08 to 0·20
D. attenuata	0·014	0·08 to 0·18
D. pruriens	0·015	0·08 to 0·14
D. acuta	0·013	0·09 to 0·15
D. hirsuta	0·018	0·05 to 0·13
D. Thwaitesii	0·013	0·05 to 0·18
D. crumenata	0·016	0·06 to 0·12
D. sylvatica	0·014	0·07 to 0·20
D. Gardneri	0·016	0·07 to 0·18
D. oppositifolia	0·014	0·08 to 0·13
D. Melanoxylon	0·017	0·07 to 0·13
D. ovalifolia	0·011	0·09 to 0·13
D. Toposia	0·013	0·06 to 0·15
D. insignis	0·014	0·06 to 0·19

The thickness of the wall varies from 0·001 to 0·0016 mm. These are the average radial dimensions and variations length of the wood parenchyma cells in the sapwood of the several species. The age of the trees and the climates under which they have grown are widely different, though the above does not show any remarkable variation.

Wood Fibres.—These compose the greater part of the secondary xylem, and are responsible to a great extent for the durability of the timber. The occurrence in large numbers of these elements of great length, with thick walls and narrow lumina, enhances the value of any timber.

These elements form large patches of tissue, often entirely filling the gap between adjacent medullary rays; at other times scattered with intervening wood parenchyma. In the heartwood the fibres form much larger and more compact areas, in radial and tangential thickness. In the sapwood one meets with relatively narrow bands of fibres, often only a single radial line of fibres existing between adjacent medullary rays.

In their vertical distribution one notes the wavy outline of individual fibres and the deviation from the vertical of their tapering ends.

The fibres are mainly in contact with like elements, or with those of the wood parenchyma on their tangential surfaces and medullary ray cells on their radial surfaces; they are rarely in direct contact with vessels, since the latter are usually surrounded by short parenchyma cells.

There is nothing remarkable in their form; they possess the normal thick or thin walls, small transverse dimensions, great vertical length, and strongly pointed ends.

The transverse outline is usually strikingly angular, and the lumina may be only partially or almost completely closed by the secondary thickening of the walls. As previously mentioned, the vertical outline is often wavy and deviates considerably from the vertical near the tapering ends.

The constancy in transverse dimensions is exhibited in these elements better than in any others; the maximum variation is however seen in the length of these elements, since they vary from that of a cambium cell to over 1 mm. in length. The thickness of the wall varies from 0·001 to 0·003 mm.

The range of variation in transverse dimensions as one passes from the heartwood to the sapwood in very old trees is very small, and this relative constancy allows one to readily distinguish the scattered fibres from other elements. A list

of measurements of transverse dimensions of the fibres in the sapwood and heartwood is given below :—

		Radial Diameter in mm. Heartwood.		Sapwood.
D. Ebenum	...	0·013	...	0·013
D. quæsita	...	0·0076	...	0·008
D. oocarpa	...	0·009	...	0·010
D. affinis	...	0·009	...	0·008
D. montana	...	0·010	...	0·009
D. Embryopteris	...	0·009	...	0·009
D. Moonii	...	0·013	...	0·013
D. attenuata	...	0·011	...	0·012
D. pruriens	...	0·013	...	0·012
D. acuta	...	0·010	...	0·009
D. hirsuta	...	0·001	...	0·014
D. Thwaitesii	...	0·011	...	0·011
D. crumenata	...	0·010	...	0·010
D. sylvatica	...	0·012	...	0·011
D. Gardneri	...	0·014	...	0·012
D. oppositifolia	...	0·013	...	0·013
D. Melanoxylon	...	0·010	...	0·011
D. ovalifolia	...	0·0075	...	0·008
D. Toposia	...	0·010	...	0·010
D. insignis	...	0·012	...	0·011

The above table would perhaps lead one to believe that our wet country species had generally larger transverse dimensions than our dry zone species. It is also to be noticed that there is not, in every case, an increase in transverse dimensions as one passes into the sapwood, and that the maximum variation in transverse dimensions for the fibres in the whole of our species is about 0·006 mm. and for fibres of the same species less than half this amount. The transverse dimensions, thickness of wall, &c., may be greatly modified by individual forces, stress, windage, &c.

Medullary Rays.—These elements are, as far as the genus Diospyros is concerned, the most variable of all the components of the secondary xylem. Fundamentally they are similar to the wood parenchyma cells since they possess thin cellulose walls and contain abundance of starch, tannin, and oxalate of lime. Their presence in abundance tends to lower the value of the timber, their thin walls and wide lumina rendering shrinking more certain.

The medullary rays occur as radial rows of cells throughout the secondary xylem. They are, in the majority of our species, only one cell in tangential width, but in some species they may be two or even three cells wide, as in D. crumenata, D. Toposia, D. insignis. D. pruriens, D. Thwaitesii, D. attenuata, and others. The occurrence of rays more than one cell in width is never general throughout the xylem, and very frequently when the double ray is traced outwards or inwards it is found to be continuous with a ray only one cell broad. There seems every probability of discovering these broader medullary rays in the xylem of nearly all our species, providing sufficient material is examined. It is usual to find that the differentiation of a medullary ray has been going on for many years without a break, but, nevertheless, several cases have been seen where the differentiation of a medullary ray has been discontinued and where new rays have appeared ; in such cases the last or first formed cell respectively is usually surrounded with fibres only, and only occasionally with a wood parenchyma cell. As one passes into the younger wood the number of rays, not necessarily the individual cells, increases, and in the sapwood of very old trees it is not unusual to find the medullary rays separated by only one or two rows of fibres, whereas in the heartwood they are usually separated by broad bands of fibres.

This increase of parenchymatous tissue lowers the value of the sapwood timber, even though the elements may be more or less filled with the brown products so abundant in the old wood. In some specimens of D. Ebenum the continuity of a medullary ray is destroyed by the intrusion of fibres on either side of the ray ; this, however, is only local, for the same ray can be seen abutting on the inner and outer surfaces of such intrusive fibre patches.

In D. insignis, where the double rays probably reach their maximum development, the distribution is very irregular, there being from two to twenty single rays between a pair

of double rays. In tracing one ray from the younger to the older wood it was first seen to be three cells broad, and very gradually one marginal row was replaced by a row of fibres, and finally, the double ray passed into a single ray, each component having a tangential diameter equal to the sum of those forming the double ray. It has also been noticed in specimens of D. attenuata, that whenever the ray is more than one cell broad the component cells are invariably of the horizontal type, and at each end of such a ray the components are of the vertical type with large tangential diameters.

It is to be noted that whenever the ray is more than one cell broad the components have always a small tangential and large radial diameter, and many sections show a double ray superposed on a broad single ray, each ray extending vertically through a distance of many cells.

The medullary rays form large vertical strands of tissue from twelve to over thirty cells in height, the components having very variable dimensions and forming part of single, double, and triple rays.

The medullary rays, since they pass through all the secondary xylem, come into direct communication with every other type of cells, but the most striking communication is with the wood parenchyma, which they so closely resemble (particularly the vertical type) in structure, thin walls and crowded contents.

Form and size can be treated better in a combined description of the differentiation of medullary ray tissue.

In nearly every species there is a well marked differentiation into (*a*) horizontal cells characterized by large radial and short tangential and vertical diameters, and (*b*) vertical cells having short radial and large tangential and vertical diameters. In many cases one feels strongly inclined to introduce yet another type having approximately the form of a cube.

In specimens of some species, notably of D. acuta and D. Gardneri, this differentiation is only feebly exhibited.

The same ray may possess members belonging to each category, but often one type exists alone throughout a considerable length of a particular ray, and is superposed vertically on a group of the opposite type.

The vertical cells usually predominate in the very old wood, and as one passes outwards the number of horizontal cells increases until in the peripheral sapwood of very old trees they are the predominant type. Sometimes the heartwood, as in specimens of D. crumenata, shows a fairly equal proportion of horizontal and vertical cells. This increasing differentiation of the horizontal type with the age of the cambium is worthy of note.

The size of the medullary ray cells invariably increases from within outwards, and this increase, since it usually results in a radial extension of the cells, leads to an increase in the number of horizontal cells. The local occurrence of rays more than one cell in width also leads to a rapid increase in the percentage number of horizontal cells.

In the sapwood of D. insignis it appears very probable that many of the horizontal cells are parts of double rays, and the vertical cells parts of single rays, the volume of the two types being nearly the same. Nevertheless, one must realize that both types of cells may be differentiated in single rays, as in D. Ebenum and others, where double rays are very scarce or do not exist.

In the sapwood of old trees the outline of the cells is usually sharply angular ; the walls are straight, and the tangential walls are frequently inclined at an angle of 45° from the vertical ; in young twigs the outline is not as sharply cornered, and tends to form a crude ellipse in transverse section.

The following table of measurements will serve to indicate the differentiation in wood of various ages in all

our species. Only the average dimensions are here given:—

Dimensions of Medullary Ray Cells in mm.

[V. = vertical. H = horizontal, medullary ray cells.]

Species.		Radial Diameter. mm.		Tangential Diameter. mm.		Vertical Length. mm.
D. Ebenum ...	V.	0·015	...	0·02	...	0·06
	H.	0·06	...	0·012	...	0·035
D. quæsita ...	V.	0·012	...	0·015	...	0·09
	H.	0·05	...	0·010	...	0·03
D. oocarpa ...	V.	0·015	...	0·014	...	0·05
	H.	0·04	...	0·012	...	0·018
D. affinis ...	V.	0·02	...	0·017	...	0·048
	H.	0·08	...	0·015	...	0·018
D. montana ...	V.	0·024	...	0·02	...	0·034
	H.	0·07	...	0·01	...	0·022
D. Embryopteris ...	V.	0·025	...	0·012	...	0·070
	H.	0·07	...	0·009	...	0·032
D. Moonii ...	V.	0·02	...	0·02	...	0·08
	H.	0·036	...	0·02	...	0·03
D. attenuata ...	V.	0·03	...	0·026	...	0·09
	H.	0·07	...	0·014	...	0·03
D. pruriens ...	V.	0.02	...	0·018	...	0·05
	H.	0 038	...	0·010	...	0·025
D. acuta ...	V.	0.017	...	0·02	...	0·054
	H.	0·050	...	0·015	...	0·027
D. hirsuta ...	V.	0·022	...	0·012	...	0·12
	H.	0.04	...	0·009	...	0·06
D. Thwaitesii ...	V.	0·024	...	0·018	...	0·078
	H.	0·08	...	0·012	...	0 023
D. crumenata ...	V.	0·019	...	0·02	...	0·06
	H.	0·05	...	0·012	...	0·02
D. sylvatica ...	V.	0·02	...	0·023	...	0·07
	H.	0.07	...	0·01	...	0·02
D. Gardneri ...	V.	0·03	...	0·02	...	0·07
	H.	0·07	...	0·015	...	0·02
D. oppositifolia ...	V.	0·019	...	0·02	...	0·07
	H.	0·055	...	0·012	...	0·015
D. Melanoxylon ...	V.	0·02	...	0·02	...	0·056
	H.	0·05	...	0·01	...	0·027
D. ovalifolia ...	V.	0·018	...	0·016	...	0·06
	H.	0·07	...	0·012	...	0·025
D. Toposia ...	V.	0·02	...	0·02	...	0·09
	H.	0·05	...	0·01	...	0·035
D. insignis ...	V.	0·03	...	0·016	...	0·08
	H.	0·056	...	0·012	...	0·018

There is, in addition to the foregoing types of parenchyma, still another which, though of rare occurrence, is worthy of description. In specimens of calamander from Karawita

forest the xylem is characterized by large radial strands, 0·09 mm. in tangential width, of very large parenchyma. These often commence at the pith and run inwards for a distance of several millimetres; they die out gradually, but frequently at the pointed end another radial patch commences and extends a considerable distance into the younger secondary xylem.

Similar strands occur in D. Gardneri from Peradeniya, the component cells being about twice the size of ordinary parenchyma and surrounded by fibres or flanked by a medullary ray. When more than one cell broad the cells are usually irregularly disposed, occasionally they exhibit a radial arrangement, though in no cases do the components exhibit the radial regularity of other elements of the secondary xylem.

The cells are parenchymatous with transverse dimensions often equal to those of the neighbouring vessels; they possess thin walls, and their contents include starch and oxalate of lime. These strands may be purely pathological, or they may perform some part in the physiology of a secondary xylem of such slow rate of growth. They cannot be regarded as parenchyma drawn from the perimedullary zone, because they appear in the sapwood of old trees; their presence in radial groups suggests an origin from the cambium similar to the broad medullary rays, and accepting this as the interpretation one must regard the final irregular disposition of the component cells as a consequence of active growth evidenced in their abnormal dimensions and numerous contents.

The Percentage Composition of the Secondary Xylem.

These calculations have been arrived at by examination of transverse sections of the secondary xylem of young twigs and the sapwood of old trees. The number of elements of each type within a fixed field of view have been counted, and after several areas have been so examined for

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each species the percentage composition has then been calculated.

Percentage Number of Elements in Diospyros Woods.

	Tracheal Element.	Fibres.	Wood Parenchyma.	Medullary Rays.
D. hirsuta.				
Young twig, 10 mm. diameter ...	1·3	74·8	7·0	16·9
Old stem, 80 mm. diameter ...	0·60	78·8	7·1	13·5
D. acuta.				
Young twig, 7 mm. diameter ...	2·1	79·8	4·9	13·2
Old stem, 60 mm. diameter ...	0·4	84·4	7·6	7·6
D. oppositifolia.				
Twig, 11 mm. diameter	2·5	75·6	5·2	16·7
Old stem, 170 mm. diameter ...	0·8	79·6	6·6	13·0
D. oocarpa.				
Twig, 6 mm. diameter ...	1·9	74·9	10·7	12·5
Stem, 255 mm. diameter	1·0	81·8	8·9	8·3
D. ovalifolia.				
Twig, 7 mm. diameter...	2·3	75·5	6·3	15·9
Old stem, 240 mm. diameter ...	1·4	85·5	6·3	6·8
D. montana.				
Twig, 8 mm. diameter ...	3·0	76·9	5·9	14·2
Old stem, 175 mm. diameter ...	1·4	81·9	7.8	8·9
D. insignis.				
Young twigs ...	3·43	75·43	2·73	18·41
Average of timber, 130 mm. diameter ...	0·85	79·00	7·90	12·25
D. Ebenum.				
Young twigs ...	2·95	73·95	8·25	14·85
Old timber, 360 mm. diameter ...	0·76	85·4	6·14	7·7
D. Moonii.				
Young twig ...	1·70	76·11	8·45	13·74
Old timber, 170 mm. diameter ...	0·94	83·60	6·53	8·93
D. pruriens.				
Young twig, 9 mm. diameter ...	1·20	74·7	12·2	12·1
Old timber, 80 mm. diameter ...	0·84	79·64	10·24	9·28

	Tracheal Element.	Fibres.	Wood Parenchyma.	Medullary Rays.
D. attenuata.				
Young twig. 6 mm. diameter ...	2·7	77·6	4·7	15·0
Old timber, 140 mm. diameter ...	0·88	83·84	3·94	11·34
D. Thwaitesii.				
Young twig, 3 mm. diameter ...	1·33	81·3	4·6	12·77
Old stem, 200 mm. ...	0·44	85·86	6·6	7·1
D. Toposia.				
Twig, 14 mm. diameter...	0·9	80·0	7·8	11·3
Old stem, 250 mm. diameter ...	0·5	81·2	7·6	10·7
D. sylvatica.				
Twig, 9 mm. diameter ...	0·8	81·0	7·1	11·1
Old stem, 405 mm. diameter ...	0·55	82·05	7·35	10·05
D. Melanoxylon.				
Twig, 10 mm. diameter...	2·9	81·2	5·1	10·8
Old stem, 270 mm. diameter ...	1·2	81·6	7·1	10·1
D. Embryopteris.				
Twig, 9 mm. diameter ...	1·2	83·3	4·3	11·2
Old stem, 310 mm. diameter ...	0·6	85·1	7·1	7·2
D. quæsita.				
Twig, 15 mm. diameter...	1·03	80·0	3·1	15·87
Old stem, 190 mm. diameter ...	0·90	85·9	5·7	7·5
D. Gardneri.				
Twig, 14 mm. diameter...	0·9	83·0	5·8	10·3
Old stem, 170 mm. diameter ...	0·7	83·0	7·5	8·8
D. crumenata.				
Twig, 20 mm. diameter...	1·0	81·4	8·8	8·8
Old stem, 210 mm. diameter ...	0·6	83·1	9·9	6·4
D. affinis.				
Twig, 9 mm. diameter ...	1·5	84·5	5·8	8·2
Old stem, 200 mm. diameter ...	0·3	91·6	3·7	4·4

This table is instructive as affording data to show the change which takes place in point of percentage number, as one passes from the oldest to the youngest xylem, and also

to give a systematic value to the percentage composition of the xylem.

Change in Percentage Number of Elements in Old and Young Xylem.—In every species the percentage number of tracheal elements decreases with the age of the cambium, the first formed xylem having the maximum percentage number and the last formed the minimum. The number of tracheal elements in the heartwood may reach 3·43 per cent. as in D. insignis, or be as low as 0·8 per cent. as in some specimens of D. sylvatica; this is a very low number, but in the sapwood it is still lower, the maximum being 1·4 per cent. in D. ovalifolia and D. montana and the minimum 0·3 per cent. in D. affinis.

Hence we see that the percentage number of tracheal elements in young and old xylem of all our Ceylon species does not vary more than 3 per cent., and the relatively low percentage number will serve to systematically diagnose the secondary xylem of our species of Diospyros. The tracheal elements are represented by a lower percentage number than any element of the parenchyma type, and this is to be correlated, perhaps, with the evergreen nature and very slow rate of growth of all the Ceylon species.

The thickest leaved species have a very low percentage of tracheal elements in the sapwood of the mature tree, as for instance D. acuta with 0·4 per cent. and D. affinis with 0·3 per cent. The thinnest leaved species in the dry zone is D. montana, with a percentage number of 1·4 in the sapwood, whereas the thinnest leaved species in the wet zone, where the temperature is never very high and the air is always moist, is D. attenuata with a percentage number of 0·88 in the sapwood of stems 140 mm. diameter.

Though knowledge of the individual variations prevents one from attaching too much importance to similar features in different species, yet it is worthy of note that in every species growing in the wet zone the percentage number of tracheal elements is approaching the minimum, as in D.

Gardneri, 0·7 per cent., D. hirsuta 0·63 per cent., and D. Thwaitesii 0·44 per cent.; whereas in the majority of our dry zone species the percentage number is considerably increased, *e.g.*, D. montana 1·4 per cent., D. ovalifolia 1·4 per cent., D. Melanoxylon 1·2 per cent.

The facts of histological differentiation are therefore in general accord with the varying climates and the transpiration which probably occurs under these conditions.

As previously shown, the decrease in percentage number from within outwards is concomitant with a regular increase in transverse dimensions.

The parenchymatous elements compose the remaining part of the secondary xylem, and are mainly represented by fibres. The fibres constitute from 74 to over 90 per cent. of the total secondary xylem elements.

The wood parenchyma, together with the medullary ray cells, tend to form an approximately constant proportion in the xylem of different ages within the same tree. Generally speaking, the percentage number of medullary ray cells decreases from within outwards, this decrease being concomitant, as in the case of the tracheal elements, with an increase in size; whereas the percentage number of wood parenchyma cells, though generally increasing from within outwards, is apt to show a steady percentage number, or even a decrease from within outwards. The approximation to a constant proportion in the old and young wood is seen in D. insignis (20·15 and 21·14), and, as pointed out in a previous paragraph, it is often very difficult, owing to feeble lignification of surrounding fibres, to be absolutely certain, in transverse sections, whether one is dealing with fibres or wood parenchyma.

Though the percentage number of wood parenchyma cells, in the majority of our species, increases in the younger wood, the difference in percentage number is rarely over 3 per cent. of the total number of xylem elements. In the xylem of D. ovalifolia, the percentage number in the wood of a young twig and the sapwood of a tree 240 mm. diameter proved

to be the same, viz., 6·3 per cent., and in other cases a reduction in percentage number has occurred in the sapwood. It is therefore obvious that the percentage number of wood parenchyma cells is the most unstable of the secondary xylem elements, since all other elements show a definite increase or decrease.

The fibres in virtue of their abundance and constitution are the most important from an economic point of view. The most parenchymatous woods, such as those of D. insignis, rarely contain less than 79 per cent. of fibres, and, on the other hand, the xylem of several species contain over 90 per cent. fibres.

From the table quoted it will be seen that the percentage number of fibres gradually increases from the heartwood to the sapwood, and in this respect is almost alone among the secondary xylem elements. The gradual increase in percentage number in passing into the younger wood is concomitant with a decrease in the percentage number of tracheal elements and medullary ray cells. The increased weight of foliage, &c., consequent on age and development is perhaps sufficient reason for the production of an increased percentage number of fibrous elements.

The percentage number of medullary ray cells comes next to those of the fibres, and varies from 6 to over 18 per cent. of the total number of xylem elements.

The highly parenchymatous woods are characterized by a particular abundance of these elements, and in all such cases the quality of the timber is inferior, as in D. insignis, D. hirsuta, and D. oppositifolia.

As with the tracheal elements, a decided reduction in percentage number occurs as one passes from the heartwood to the sapwood, but this is accompanied by an increase in dimensions, especially in the radial direction. In the sapwood of most species the enormous size of these elements is apt to create an erroneous idea of their percentage number; the decrease in the latter is fully compensated by the increased dimensions.

Rings of Growth.

These are inconspicuous in the majority of our species. According to Ursprung the timber of some species of Diospyros presents well defined rings of growth when the trees have been grown under a subtemperate climate.

The whole of our Ceylon species are characterized by a slow rate of cambial activity, and, with the exception of the partially deciduous trees of D. montana and D. ovalifolia, may be regarded as typical evergreens. Nevertheless, the majority of our species are characterized by foliar periodicities which recur, fairly regularly, year by year, and these together with the independent effects of a hot dry season, are perhaps responsible for the zoned differentiation often met with. We have also to allow for the possibility of special periods of activity determined by internal forces and expressed in the differentiation of irregular patches of xylem. In the majority of the specimens examined the inconspicuous rings have been difficult to follow throughout the whole of any transverse section, many being tangential bands in association with a neighbouring branch, and therefore roughly limited to the side on which the branch occurred. In timber of D. insignis and D. Thwaitesii rings of growth are visible to the naked eye, and consist of broad dark bands alternating with narrower bands of a lighter colour. The narrow light rings vary from 0·2 mm. to 1·2 mm. in radial diameter, and are disposed at very varying distances—radially—from each other.

The rings of growth are often present in one part of the section and gradually merge into adjacent rings of growth, and in consequence of this, and the varying radial distances (2 to 8 mm.) between successive rings, we find that the number of rings along different radii is subject to great variation. It is impossible to at present determine in our Ceylon ebonies the exact representation of time of each ring of growth.

Rate of Growth.

The genus Diospyros, in Ceylon, possesses some of the most slowly-growing tropical trees. In the seedling and sapling stages, up to the first ten or twelve months the growth takes place at a fairly rapid rate; seedlings two months old may measure, above ground, from 30 to 150 mm. according to the length of the hypocotyl, but in two and a half years the total height may exceed 3,300 mm.; saplings ten years old may measure less than this, and the subsequent growth takes place at a slow rate. The following are the dimensions of two and a half years old saplings raised in the same plot at Peradeniya:—

Species.		Height. mm.		Circumference. mm.
D. montana	...	3,610 (11 ft. 10 in.)	...	111
D. Ebenum	...	1,828 (6 ft.)	...	84
D. Embryopteris	...	1,220 (4 ft.)	...	81
D. quæsita	...	610 (2 ft.)	...	38

Some species never develop into large trees, *e.g.*, D. acuta and D. pruriens, but the majority of Ceylon species attain huge dimensions, particularly D. sylvatica, D. crumenata, and D. affinis. There are, however, very few trees of known age, and exact information cannot therefore be obtained. There is one specimen of D. quæsita in the gardens, which, though known to be over sixty years old, measures only 472 mm. in circumference and a total height of about 14 metres; this, however, is one of our slowest growing species; other species, notably D. Embryopteris and D. montana, probably grow at a much quicker rate.

Sample plots for observing the rate of growth have been established by the Ceylon Forest Department, and yearly observations have been made on selected trees in the various forests; the results are, however, at great variance.

Broun states that after reaching a circumference of 914 mm. (3 feet) D. Ebenum is very slow growing, and that the tree may reach a circumference of 457 mm. (1 foot 6 inches) at the age of 25 years, 914 mm. (3 feet) at 75 years, 1,372 mm. (4

feet 6 inches) at 135 years, and 1,828 mm. (6 feet) at the age of 200 years.

The following observations were made on trees growing in the Peradeniya Garden :—

Circumference of Trees in Millimetres.

Date of Observation.	D. Embryopteris. mm.	D. Gardneri. mm.	D. Ebenum. mm.	D. quæsita. mm.
August 13, 1900...	585	467	147	370
January 1, 1901 ...	587	468	147	382
July 2, 1901 ...	600	468	156	400
August 6, 1902 ...	630	474	162	430
August 12, 1903...	673	496	179	472
Increase in circumference in three years ...	88	29	32	102

The selected trees were of unknown age, and, as is shown in the first measurements, of widely different dimensions ; it is, nevertheless, of interest to know that in trees of the selected species the increase in circumference may be from 29 to 102 mm. in three years' time. This increase may be due to phellogenetic activity as much as that of the vascular cambium, but assuming that the increase in circumference is due to the production of secondary xylem only, we find that that in D. Ebenum is equal only to 62 vessels, or an average of one to two vessels along each radius, per month during the three years in question.

Timber.

The genus Diospyros has obtained its widespread recognition mainly in virtue of the valuable timber yielded by several of its species. The term *ebony* is loosely applied to any black heavy wood capable of taking a good polish, and from time to time there has been considerable discussion as to the exact botanical source of the ebony of the ancients. Many plants are known to yield timber which in colour and density resembles the real ebony, and botanists have been found who assert that the ebony of the ancients was not

obtained from the genus Diospyros, but from a leguminous species, called Fornasinia ebenifera, Bertol. The natural order Leguminosæ has long been known to yield variously coloured timbers, and in some countries the respective species furnish a marketable ebony, *e.g.*, Dalbergia Melanoxylon, G. and P., the ebony of tropical Africa, and Brya Ebenus, DC., the Jamaica ebony.

In Ceylon, however, the ebony of export is obtained exclusively from species of Diospyros, and mainly from the trunks of D. Ebenum. This ebony has been known from distant times, and some botanists believe that the ebony mentioned in the Bible was obtained from this Island.

According to Trimen* the tree was not known to Hermann, and only the timber of it to Burmann,† who quotes from Grimm‡ as to its medicinal virtues.

Rumph§ states that ebony trees are abundant about "Trinkenemale," and Trimen believed this to be the earliest record of our most important ebony-yielding trees in Ceylon.

The ebony is obtained by felling the tree and stripping off the peripheral sapwood. It is usual to fell all those trees which have attained or exceeded a breast-height circumference of 2 metres (6½ feet), providing the preliminary examination indicates the existence of a good proportion of solid black heartwood. The preliminary examination usually consists of making an incision and determining the extent to which the discolouration has proceeded; in some cases an apparatus known as Pressler's increment borer is used, as by this means only the minimum damage is done to the timber, and the tube can be easily withdrawn and the cylinder of wood extracted from the stem. In Ceylon the felling of the ebony trees is carried out on definite principles, each officer clearing only those trees which have

* Trimen, Flora, Vol. III., p. 95.

† J. Burmann, Thesaurus Zeylanicus, 1647.

‡ Grimm, Laboratorium Ceylanicum, 1679.

§ G. E. Rumphius, Herbarium Amboinense, 1750.

attained the standard dimensions, and at such a rate that only one-fortieth to one-sixtieth of the forest acreage under his charge is cleared each year.

The occurrence of ebony within the plant cannot be stated in terms of the age of the tree, the dimensions of the stem, or the climatic conditions under which the plants have been grown, though a few facts capable of a very general application may be here given. The black heartwood occurs usually in the stem, but is often present in young twigs and roots. In the majority of our species the discolouration commences in the perimedullary zone and spreads from within outwards. The discolouration is usually of an uniform black in D. Ebenum, streaked in D. oocarpa, D. affinis, D. quæsita and others, red in D. Moonii, and a dirty white in such species as D. insignis and D. attenuata. The discolouration may occur in the oldest central wood only, or it may appear in local strands throughout the secondary xylem of the stem. In many young stems the only areas where ebony has been produced are directly associated with insect punctures, wounds, &c.

The occurrence of the central black wood within the length of the stem is often erratic, though most usually it decreases in volume from below upwards.

The eccentric formation is where the central column of black wood widens and narrows repeatedly at different points along the stem, and in consequence of this one cannot accurately estimate the volume of ebony in a stem by external observations alone. In some instances, particularly in young stems and twigs, the black heartwood repeatedly dies away and reappears at different points along a given length.

The age of a particular tree or the dimensions it has attained do not afford a sure criterion as to the quantity of ebony it will possess, though the probabilities are that the older the tree and the larger the dimensions, the greater will be the proportion of discoloured heartwood. This

uncertainty has long been recognized by persons engaged in financial speculations, and too much stress cannot be laid on the individual variation which occurs in trees of the same species from the same or different localities.

On the other hand, there can be no question as to the specific tendencies to produce a definite type of heartwood, though even here one has to allow a wide range of variability for each species. For instance, the heartwood of D. Melanoxylon and D. Ebenum is almost invariably jet black, and on this account these two species provide the greater part of ebony from India and Ceylon; D. insignis, on the other hand, never yields a black heartwood, D. Gardneri always produces a yellow wood, and D. Moonii a timber which is of a red tint spotted here and there with small black strands. There could be no possible doubt of the species were the timbers of D. Ebenum, D. Kurzii, D. insignis, and D. quæsita to be mixed with one another, as their macroscopic characters are so pronounced.

The specific colour tendencies are somewhat difficult to explain. The two factors which determine the colour of the timber in the respective species are: (1) the means of distribution of the coloured substances; (2) the proportion of coloured gum and resin present in the tissues.

It is perhaps safe to assume that the best or most general distribution of coloured substances will be effected in those xylems the elements of which are freely communicating with one another, and therefore those species the timbers of which contain a high percentage of medullary ray cells and wood parenchyma should show the most general distribution of colouring substances. The fact that the xylem of D. insignis is highly parenchymatous and is really white points to the conclusion that for the production of ebony the superabundance of colouring material is the first desideratum, rather than profusely pitted elements. An open type of pit communication between the elements will tend to prevent the formation of central ebony in timbers where the colouring

substances are not abundant. The central timber will tend to become dark in colour when the communication between the elements is not frequent, as the substances must then remain in approximately the same area in which they were formed.

The jet black colour of the timber of species such as D. Ebenum is due to the coloured substances being present in large quantities in the oldest wood and remaining approximately in that area, If a more open communication existed between the elements in this species the colouring materials would be more widely distributed and the central timber deteriorate in consequence.

The red, yellow, or white colour of many Diospyros timbers is due either to the more complete distribution of the colouring substances throughout the wood in the respective species or to the relative scarcity of coloured substances.

The climate does not appear to have any appreciable influence on the production of discoloured heartwood, the same species showing similar characters in the dry, wet, and intermediate zones of Ceylon. The majority of our ebony is obtained from the dry zones in the northern part of Ceylon, because D. Ebenum grows more luxuriantly there than elsewhere, and not because the black timber of this species is more abundant, per tree, or of better quality than that from the scattered trees of the wet zone.

It is, however, generally believed by Ceylon foresters that the nature of the soil exerts some influence on the proportion of discoloured wood. Many cases have occurred where the trees growing on rocky hill banks possessed large quantities of black heartwood, and the proportion of ebony decreased as one got on to better soil. According to Broun the best ebony in Ceylon is found on rocky well-drained soil. It grows well on soils containing a large quantity of clay and on sandy loam with a good subsoil drainage.

The general belief is that the proportion of discoloured heartwood tends to increase in trees grown on poor rocky soil. This is substantiated by every forester I have met.

The durability of our Diospyros timbers is due to the nature and percentage number of the elements comprising the wood, together with the presence of coloured contents partially or wholly filling the elements. In all our Ceylon species of Diospyros the cambium divides very slowly, and the elements, particularly the fibres, possess small transverse dimensions and thick walls ; the percentage number of fibres is in every case very high, and that of the tracheal elements very low, consequently the xylem is much more durable than the majority of our Ceylon timbers. Nevertheless, the histological composition of the secondary xylem is only one factor in determining the durability of these timbers, the infiltrated gums and resin providing a substantial support to the otherwise empty elements. The relative durability of the outer white sapwood and the central ebony is well seen in trunks of trees exposed to the atmosphere and vermin ; the sapwood is stripped completely in a few years, leaving a smooth black log of ebony which resists the attacks of ants and many wood borers.

Discolouration of Timber.

The discolouration of the wood is mainly due to chemical and physical changes of the materials stored in the elements of the wood, and to a less extent to a change in composition and colour of the cell walls. The coloured material entirely fills the lumina of the elements in pure ebony, and decreases in quantity as one passes to the red, yellow, and white woods. The white sapwood surrounding the central ebony contains a varying quantity of coloured material partially filling the secondary elements, and the quantity of this material increases from without inwards.

To the naked eye there appears to be a sharp distinction between the limit of the central ebony and the white sapwood. A gradual series of changes can, however, be discerned in microscopic sections, and for the conversion of the peripheral sapwood into ebony it is mainly a question of time.

Usually the ebony or heartwood occurs as a fairly regular circular mass at any particular level in the stem ; when the ebony is not limited to xylem of the same age the projections towards the sapwood are associated with wounds or old branches.

To explain why the limiting line of the central ebony is so sharply defined, or, in other words, to explain why the coloured substances occur so definitely in xylem of the same age, we must consider the distribution and pit communication between the different elements. In the first place we must admit that the wood parenchyma, medullary ray cells, and tracheal elements are abundantly supplied with large pits on all surfaces, whereas fibres are but sparsely pitted.

The tangential bands of wood parenchyma serve as excellent means for the transference of coloured substances through xylem of the same age, from like cells or those of the medullary ray to the tracheal elements or the short parenchyma surrounding them.

The frequency of the pits between the wood parenchyma, medullary ray cells, and tracheal elements is one reason why the circulation of the coloured substances, originating in the parenchymatous elements, should tend to keep within these elements. The fewness of pits in the fibres does, on the other hand, account for their sparse contents and the fact that they are the last elements to have their lumina filled with the coloured substances.

We therefore see that the maximum facility is accorded for transference of the coloured substances tangentially through the wood parenchyma and tracheal elements rather than radially through the wide patches of sparsely pitted fibres, and this will perhaps serve to explain why the coloured substances tend to first fill the elements in xylem of approximately the same age and thus lead to the sharp line of distinction between the outer limit of the ebony and the white sapwood.

At the same time the transference of coloured materials can and does take place in the radial direction, from one

medullary ray cell to another, but the proportion of these elements is so small compared with the surrounding fibres, that any contents they may possess cannot greatly change the tint of the xylem as a whole.

When the parenchymatous and tracheal elements have their lumina blocked the coloured material gradually infiltrates into the fibres. The coloured substances, under normal circumstances, first appear in the oldest elements, and therefore the blackening takes place from within outwards.

The composition and origin of the discolouring substances has been discussed by Belohonbek, Hartig, Molisch, and Moeller. They all regard the coloured materials as being singular in chemical constitution, and the terms "gum" and "resin" have been frequently applied to the separated substances.

The coloured substance is partially soluble in water, creosote, benzine, ether, and sulphuric acid. The solution varies in colour from a deep brown to claret red. In all cases microscopic examination of the sections so treated shows that only a very small proportion of the coloured substance has been extracted. If the sections are treated with strong sulphuric acid for several days the walls of the elements disappear and liberate long black rods of material which resist the attack of the strong acid even after heating. These black carbon-like rods appear to be unaffected after treatment with any reagent. Mr. Kelway Bamber has very kindly made an analysis of the coloured timber, and has allowed me to quote his results here:

Ebony Dust.

	Per cent.
Moisture ...	14·36
Organic matter...	77·84
Ash ...	7·80
	100·00

	Per cent.
Water extract (soluble gum) ...	3·60
5 per cent. NaOH extract ...	7·24
Residue (dark rods) ...	67·00
Ash in residue ...	7·02

Mr. Bamber finds that the 5 per cent. caustic soda solution contains a gum precipitable by alcohol, and a resinous body,

dark reddish brown in colour, which can be extracted from the original ebony dust with alcohol and amounts to 3·58 per cent. of the dust.

The black colouring material therefore contains two gums, one resin, and an insoluble residue composed mainly of carbon.

It has been asserted that the colouring materials arise by chemical change of the inner layer of the elements in which they occur, and even Molisch believed that the reputed thinness of the walls of some vessels was due to part of the material having been so modified. My own observations do not confirm this theory, though I have noticed a certain amount of swelling when sections of the fresh wood are placed in water. This is probably due to the absorption of water by the thin layer of gum which forms a lining to the tracheal elements, and which occurs in the yellow or white sapwood of ebony-bearing species.

From an examination of longitudinal sections of the sapwood and heartwood of our species I have concluded that the greater part, if not the whole, of the coloured materials filling the lumina of the elements is derived from the materials accumulated in the parenchymatous system of the secondary wood. Usually the discolouring substances make their first appearance in the cells of the medullary ray or wood parenchyma, then in the tracheal elements, and lastly in the fibres.

The parenchymatous elements of the sapwood are invariably packed with starch grains, tannin, and calcium oxalate. The starch grains gradually lose their regular outline and a fine granular texture becomes obvious, together with a change in colour. Finally, globules suggestive of a resin or gum appear in the parenchyma cells, and as these increase a deepening of tint from yellow to brown occurs. It would therefore appear that by a series of chemical changes the contents of these elements gradually disintegrate, and the resulting compounds are in the form of globules of coloured material. It must, however, be remembered that starch is a stable

substance, and also that the disappearance of many grains is due to their conversion into sugar for uses within the plant, and may not be associated with the coloured globules under consideration. If one examines the vessels of the sapwood one often finds the globular material entering through the pits. In one section the stream of coloured material could be traced from the medullary ray cells through the pits into the lumen of the wide vessel with which they were in contact.

In very many cases the coloured substances project into the lumen of the vessel as large globules suggesting tyloses; these swell, and are partially soluble in water. The globules may exhibit stratification according to the colour of the different parts.

In other cases the large globules are entirely absent, and the deposit appears as a thin film of a pale straw-coloured material in the area of the pits. The whole of the pits in the wall of any particular vessel do not usually present this appearance, the pits thus coloured usually occurring only in local groups along the wall of the vessel. The deposit may become very abundant, and when half filling the vessel is irregularly globular in outline. It therefore appears that the material occurring in the tracheal elements is derived from the substances stored in the parenchymatous elements, and the relative freedom of the latter from contents—a feature often noticeable in mature ebony—may be a consequence of exhaustion of store material. The infiltrating material may be of a pale straw or light brown colour; as it increases in quantity the tint deepens and the elements finally become blocked with deep brown or black material.

The gum-resin issues in large quantities from the stumps of freshly felled trees and accumulates at points of exposure. The walls of the elements from trees which have yielded large quantities of this substance do not show any reduction in thickness, and it is probable that they have been derived from disintegration of store materials in the parenchyma of the wood.

The stratification exhibited by the deposit is due to the variation in the colour of the different parts, and may be detected in the globules formed within the parenchymatous elements.

The maximum quantity of gum-resin is seen in our blackest woods, such as D. Melanoxylon and D. Ebenum, and the minimum in our whitest woods, such as D. insignis and D. hirsuta.

The mottled colour of some timber specimens is due to the gum-resin being almost limited to the medullary ray cells; these are packed with the brown-coloured substances, while the neighbouring elements, including vessels, are nearly empty. This feature is noticeable in our lighter coloured woods, such as D. Gardneri, D. sylvatica, and D. insignis.

The appearance of the material in the vessels may occur unaccompanied by any change in the physical properties of the wall, and the fuchsin and safranin reagents can still be used with advantage, even when the elements are entirely filled with the coloured substances. In many cases the coloured substances impregnate the walls of the elements, but only in few cases do the walls show signs of decay.

V.—SEEDLINGS.

In the development and anatomy of the seedlings several interesting points have been determined, and a synopsis is here given. The characters of seedlings have not yet found a prominent place, if one at all, in systematic monographs. The occurrence of specific and generic characters in the developmental phases, in the morphology of the cotyledons and epicotyledonary leaves, and in the behaviour of the leaf traces must serve as the reasons for their inclusion in the present work.

The importance of seedling characters for systematic purposes has of late been discussed by various botanists.

Miss Sargant* has stated that no doubt remains as to the systematic value of the indications given by the vascular

* Ethel Sargant, The Origin of the Seed-leaf in Monocotyledons; New Phytologist. Vol. I., No. 5, 1902.

structure of the cotyledon, hypocotyl, and primary root. At a later date* a further contribution was made on the same subject, and in it a very great significance was alleged for seedling characters. Though the examination was mainly with seedlings of the Liliaceæ and Ranunculaceæ, the evidence seemed sufficient to justify the publication of a theory of the origin of monocotyledons founded primarily on the structure of their seedlings. This theory was again discussed at the British Association meeting, September, 1903. Fritsch,† in a general discussion on the value of anatomical characters, states that though seedlings may present a very uniform type of structure throughout large groups, the anatomy of the seedling may be expected to indicate affinities more clearly than that of any other part of the plant.

The length of the hypocotyl and primary epicotyledonary axis, the phyllotaxy, and general morphology of the first formed leaves, together with the persistence or dropping of the cotyledons, provide ample material for the recognition of most Ceylon species of Diospyros. In addition to these characters we have to consider the number of traces per cotyledon, and the behaviour of the epicotyledonary and cotyledonary traces in the hypocotyl and primary root; these in themselves afford facts sufficient to allow one to construct a useful artificial key for the identification of Ceylon species.

Germination.—The time taken for germination varies according to the condition of the seeds when gathered and sown. If sown after partial drying in air, germination usually occurs within two to four weeks. If, however, the fresh seeds are sown direct, without drying, it may take several months before the primary root projects from the micropyle. The seeds of D. ovalifolia have a particularly

* Ethel Sargant, A Theory of the Origin of Monocotyledons founded on the Structure of their Seedlings; Ann. Bot., Vol. XVII., No. LXV., January, 1903.

† F. E. Fritsch, The use of Anatomical Characters for Systematic Purposes: New Phytologist, Vol. II., No. 8, October, 1903.

hard testa and a copious horny endosperm, and many do not germinate until nine months after sowing.

The material required for the study of the vascular system prior to the production of secondary elements is best obtained by allowing the seeds to germinate on sheets of blotting paper, which are always kept moist, or on porcelain dishes partially immersed in water and covered by a bell jar.

If it is desirable to study the embryo prior to the appearance of lignification of the proto-elements, a convenient method is to first thoroughly dry the seeds until the testa begins to crack and then immerse them in water kept at 100° F. for some time. Seeds of D. Ebenum treated in this way provided excellent material, since the embryos completely emerged from the confines of the endosperm into the bath without being injured in any way.

Development of the Seedling.

When the primary root has attained a length of 2 or 3 cm. the young curved hypocotyl appears above ground. The cotyledons are embedded within the copious endosperm, and together with the testa are still below the surface of the ground. Subsequently the hypocotyl shows signs of rapid growth, the collet area increases in thickness, and the hypocotyl becomes more strongly arched and sooner or later assumes an erect position, carrying at its apex the cotyledons or epicotyledonary leaves. In every Ceylon species of Diospyros and also Maba, the seedlings are of the epigeal type, though the mode of development in those species having very short hypocotyls is suggestive of a hypogeal habit.

In a few of our species, viz., D. Ebenum, D. Gardneri, D. sylvatica, and D. montana, the pair of opposite ovate cotyledons persist for many months and function as assimilatory structures until an adequate system of epicotyledonary leaves has been established. In all such cases the epicotyledonary leaves develop very slowly. This is true for seedlings

raised from seed obtained from cultivated trees in India and Ceylon and from the jungle. The delayed epicotyledonary development is characteristic only of those species which have normal persistent cotyledons. It is also to be noticed that in all these cases the primary epicotyledonary axis, *i.e.*, axis between cotyledonary node and first epicotyl leaf, is very short, and that the first two leaves on this axis never form an opposite pair, but are always arranged alternately, and are speedily followed by many others disposed in a similar way.

The majority of our Ceylon Diospyros species exhibit a curious mode of development, and a detailed account of seedlings of D. quæsita is now given, commencing at the stage of the strongly arched hypocotyl, when the testa, endosperm, and cotyledons are still connected with the hypocotyl and partially covered with soil. At this stage the testa splits near the micropyle, and the gap thus formed gradually extends along each side of the seed to a distance of about 1 cm. The chalazal end and often the greater part of the seed is still below the surface of the soil. In consequence of the strain set up by the rapidly growing hypocotyl the sessile cotyledons now become detached and the hypocotyl frees itself from the confines of the seed, carrying the enhanced epicotyledonary leaves at its apex. The cotyledons are left behind surrounded by the bulky endosperm, and from the moment of their detachment the young seedling receives no further nutritive substances from the endosperm. At this stage there is a large quantity of endosperm, and this, together with the whole of the reserve materials contained in the parenchyma of the cotyledons, is wasted. In consequence of the detachment of the cotyledons and the enhanced development of the epicotyledonary leaves a large number of the seedlings die. This is brought about by the death and decomposition of the cells of the detached cotyledons and the endosperm, which in time leads to a diseased condition of the apex of the epicotyledonary axis. It is therefore highly desirable to apply artificial pressure and crack the

testa sufficiently to allow the cotyledons to escape prior to detachment.

The cotyledons, though they have attained their full dimensions and are exposed to light, never take on the work of assimilation as in the case of the species with normal persistent cotyledons. They are at first pale yellow in colour, but within twenty-four hours show signs of death, and within thirty-six hours become black and shrivelled. They may, however, still adhere to the cotyledonary node by the bases of their short petioles.

The point of interest in this curious suicidal mode of development is that the disconnection of the cotyledons seems to have been provided for long before the actual detachment takes place. Ungerminated embryos show a conspicuous epicotyledonary axis usually with a minute pair of interlocked leaves at the apex. In those species with persistent cotyledons such an enhanced epicotyledonary development does not present itself until three or even five months subsequent to the full exposure of the cotyledons. By the time the cotyledons are detached the epicotyledonary leaves are well developed ; they are also provided with a palisade tissue, and on exposure take on the work of assimilation usually allotted to the cotyledons. Furthermore, the first epicotyl leaves usually form an opposite pair of interlocked leaves, and thus remind one still more forcibly of cotyledons. When the epicotyl leaves form an opposite pair these usually persist alone for many months ; this suggests most strikingly that their enhanced development has really been an effort, and internal evidence indicates that it is associated with abortion of cotyledons, which appears to have been taking place through many generations.

The majority of our species show this detachment of cotyledons and enhanced development of epicotyledonary leaves which take on the work usually assigned to cotyledons. The cotyledons never acquire palisade tissue, but this layer

is laid down in the epicotyledonary leaves long before they are exposed to light.

As to the causes which lead to the detachment of the cotyledons, it is very difficult to make any definite statements. The regularity of the occurrence in seeds of all sizes, under natural and artificial conditions, is suggestive of the possibility of a definite cellular activity cutting off the cotyledons at the node in a manner similar to that in which old leaves are cut off from the parent tree. This, however, cannot be the case, as in all experiments where the cotyledons have been set free prior to detachment their dead and shrivelled tissues have persisted at the cotyledonary node for a considerable length of time.

Hence we are driven to the conclusion that the detachment is probably a case of separation under conditions of strain, and several possible factors may be quoted in support of this contention. The first is the pressure of the endosperm. In those species where the cotyledons are persistent the endosperm may be equable (D. Ebenum) or strongly ruminate (D. sylvatica) ; similarly it may be markedly ruminate in species with detached cotyledons (D. hirsuta) or equable (D. insignis). Hence, the pressure of the endosperm, as indicated by the absence or presence of ruminations of this substance, has probably very little to do with the detachment of the cotyledons. A second factor is probably to be obtained in the bulk of the endosperm, testa, &c. ; for though D. ovalifolia may prove exceptional, it is a fact that those species with persistent cotyledons have relatively a smaller quantity of endosperm which is necessarily exhausted early, resulting in a shrinking of the testa and liberation of the cotyledons at an early date.

However, neither of the foregoing, even if coupled with the increased resistance of the irregular surface of the mature cotyledons, can completely explain the cause of detachment.

The chief cause, in my opinion, is to be found in the insufficient splitting of the testa ; in D. pruriens and D.

ovalifolia there is no splitting of the testa, and it is impossible for an expanded cotyledon to effect its exit from such a small circular micropylar opening amply filled by the thin axis of the hypocotyl ; in other species there is only a partial splitting, and even in calamander seeds the gap is never large enough to allow the cotyledons to escape intact.

Since the splitting of the testa would be more complete if the endosperm were exhausted more quickly, it follows that probably all the forces mentioned above play some part in the final detachment of the cotyledons.

The mode of development just described is not a consequence of the artificial raising of the seeds ; the detachment occurs in nature, and the internal characters of the epicotyledonary and cotyledonary traces indicate that this line of development has been habitual for a considerable period of time. This mode of development is characteristic of some of our rarest species, and is probably one of the factors which is leading to the extinction of many species.

The detachment of the cotyledons is attended with the minimum disadvantages in those species having short hypocotyls (D. insignis and D. Embryopteris). In these instances the seed coat, endosperm, and cotyledons are but rarely raised above the surface of the soil, and the young though enhanced epicotyledonary parts gain easy exit.

The habit of D. insignis in particular is very suggestive of a hypogeal tendency, since the seeds are rarely raised above ground, the hypocotyl is very short, and the epicotyl stem very long and provided with small leaf rudiments suggestive of typical Garcinia seedlings.

The morphological relationships of the parts of the seedlings are also of interest. In the first case it is worthy of note that in those species possessing short hypocotyls the epicotyledonary axis is usually long (4 to 7 cm.), whereas in those having hypocotyls of normal length the epicotyledonary axis is usually only from 0·5 to 1·5 cm. in length.

By this coincidence the first series of pronounced epicotyledonary leaves are brought to approximately the same height above ground in all species.

The lengths of these axes are fairly constant in each species, the median length of hypocotyls being from 5 to 7 cm. as in D. Ebenum and D. Thwaitesii ; short hypocotyls, about 1 to 2 cm. as in D. insignis ; and long hypocotyls, being from 10 to 11 cm., as in D. crumenata and D. quæsita.

The cotyledons are in all cases of the broad ovate type with blunt or tapering apices and attached by very short petioles at the cotyledonary node.

The first epicotyledonary leaves are, in the majority of our species, opposite ; in one species they may be opposite or sub-opposite, and in the remaining species they are alternately disposed on an elongated axis. In all cases the leaves are simple, ovate-lanceolate in shape, but show differences in size and venation in the respective species. Generally speaking, they possess the diagnostic feature of the leaves of the mature plant in all points except size.

Internal Characters of the Seedlings.

In every species the number of traces per cotyledon is constant, and we have to separate those possessing two traces per cotyledon (*e.g.*, D. Ebenum and D. Gardneri), from those with three (*e.g.*, D. crumenata and D. Embryopteris).

In those possessing two traces per cotyledon the cotyledons are usually persistent ; the cotyledonary traces are prolonged into the primary root and the epicotyledonary traces die away immediately below the cotyledonary node.

In those species with three traces per cotyledon the majority are characterized by detachment of cotyledons and enhanced epicotyledonary development, and though there are three traces per cotyledon the xylem and phloem of the median trace are abortive in all species except D. pruriens.

Furthermore, in those species with deciduous cotyledons the epicotyledonary traces are continued through the hypocotyl into the primary root.

The tendency for the median cotyledonary trace to abort is what one may expect in those species where the cotyledons are defunct at such an early period, and the prolongation of the epicotyl traces into the root is rendered necessary since nutritive substances cannot be absorbed from the endosperm. The fact that the embryo shows these structures fully differentiated points to a past history in connection with these curious developments.

The traces of the cotyledons are provided for the conduction of food materials absorbed from the endosperm to all parts of the seedling; in those species with persistent cotyledons they are the only vascular tissues present during the first few weeks or months of the seedling's life. If the absorbing tissues and the reserve food are cut off from the seedling during this phase, the young plant must die if the epicotyledonary traces are not prolonged into the root to establish a connection between the growing point of the stem and the new absorbing tissues constituted by the primary root.

It is very doubtful whether such developments can be accomplished in one generation, and the definiteness of the median trace abortion and epicotyledonary prolongation are sufficient evidence that the curious mode of development has been going on for many generations past.

There are, however, several facts which point to a very unstable condition. Seedlings of the same species show considerable variation in the degree of differentiation of the different tissues, and also in the behaviour of the vascular strands in the region of the collet. In one seedling the epicotyledonary and median cotyledonary traces were absent from the primary root at a distance of 2 cm. from the apex; at this point only the four lateral cotyledonary traces were present, though in the hypocotyl the six cotyledonary and two epicotyledonary bundles were in evidence; in this case the median cotyledonary trace had apparently suffered complete abortion at a point which had not yet been reached

by the descending epicotyledonary trace, and thus indicated one of the possible stages in the establishment of a new root symmetry.

Splitting of Xylem Traces.—Another point which indicates most markedly the unstable conditions of the seedlings is seen in the splitting of the xylem of the leaf traces. This is best seen in seedlings which are very young and in which vascular cambium has not made its appearance, and for the sake of clearness a description of the behaviour in D. Embryopteris is here given. At the cotyledonary node three vascular bundles make their exit on each side and persist as three separate strands in the petiole of each cotyledon. At right angles to the cotyledons, two strands from the epicotyl leaves appear, one on each side. As these strands are traced through the hypocotyl they are seen to separate from one another, and on reaching the collet area where the parenchymatous system is large each xylem strand separates into two, three, or more parts. At the collet area I have counted as many as twenty-two groups of xylem resulting from the scattering of the original eight traces. Traced below the collet into the primary root a fusion occurs, but whether this takes place between parts of dissimilar bundles or otherwise is very difficult to determine. The fusion goes on gradually, and at certain levels the number of strands is seen to be sixteen, later twelve, and through eight and six on to a final four. In no species are there ever less than four strands in the apical portion of the primary root.

Owing to the highly scattered nature of the xylem elements it is often impossible to ascertain the exact area wherein the inversion of orientation is effected.

In seedlings of the same species there is a great variation; sometimes only one lateral cotyledonary trace undergoes division, sometimes all three; the epicotyledonary traces when present may remain compact, or each may separate into two or three strands. In a general way it may be stated that the type of xylem in the seedlings is one where a splitting is seen in any of the cotyledonary traces into two or

three portions, together with a prolongation of epicotyledonary strands to different distances in the primary root.

In seedlings where the epicotyledonary traces are not continued into the primary root a similar splitting of the xylem of each cotyledon trace may occur.

The presence of twelve to twenty-two xylem strands in a comparatively narrow cylinder, where each strand is relatively large, renders the actual behaviour of each strand difficult to follow.

The reason for such profuse scattering of the proto-xylem system is perhaps to be found in the bulky nature of the parenchymatous system. In all cases the scattered condition attains its maximum in the collet area where the parenchymatous system is at the maximum, and it would appear probable that the mechanical support and supply of nutrition were the objects aimed at. The splitting is always more complicated in a wide parenchymatous seedling, such as D. Embryopteris, than in a narrow one, such as D. Ebenum, and the fact that the strands are thus distributed prior to the appearance of a vascular cambium is sufficient proof that the diffuse condition of the proto-xylem is not due to the pressure of new cambial products.

Direction of Lignification and Differentiation of the Vascular Elements.

If the embryo or young seedling be examined the differentiation of lignified elements can be determined. We may assume that lignification commences in the oldest element first and gradually appears in successively younger elements. *i.e.*, that the direction of differentiation of the elements is the same as that of lignification. In the embryo the beginning of lignification is seen in the xylem of the cotyledonary traces, and commencing at the cotyledonary node the lignified elements can be traced downwards into the primary root and upwards into the petiole of the cotyledons. The lignification at this stage is somewhat irregular, and appears to be a little

advanced in the median cotyledonary trace as compared with the laterals.

In the short axis of the embryo it is difficult to fix on the exact area at which lignification first appears. Examination of later stages shows the maximum lignification of the cotyledonary xylem at the collet area, and that the lignification subsequently spreads downwards into the primary root and upwards into the hypocotyl. The collet area is also the first to show a vascular cambium and the maximum parenchymatous system; it therefore appears to be the centre of activity of the seedling axis.

The fact that the lignification of the cotyledonary xylem reaches the maximum at the collet area may, however, still allow of the original starting point being at the cotyledonary node, and the enhanced lignification at the collet may be a secondary development associated with the requirements of the seedling subsequent to the purely embryonic stage. In the embryo the conducting systems are functioning in the conveyance of nutritive materials from the endosperm to the primary axis, and there does not therefore appear to be any necessity for lignification to commence at the collet area. There is the possibility that the direction of lignification may be purely responsive to the requirements of the seedlings, in which case no evidence can be obtained of the direction of differentiation of the original xylem elements.

The lignification is completed throughout the hypocotyl and primary root of the embryo within such a period, that prior to the apex of the primary root presenting itself at the micropyle a continuous series of lignified elements exist from root to cotyledons.

The epicotyledonary strands when present in the primary root show a definite direction of differentiation.

The phloem of each epicotyledonary strand begins at the epicotyl leaf and spreads downwards into the hypocotyl and root. This direction of differentiation is obviously the best,

since the function of the phloem strands is to conduct the materials prepared in the epicotyl leaves, together with the endosperm material absorbed through the epidermis of the young stem, to other parts of the seedling, viz., the hypocotyl and root.

The xylem of the epicotyledonary traces is, however, judging by the direction of lignification, differentiated in the opposite direction. This is obviously the best direction possible, as these tissues have to conduct the water from the root area to the epicotyl leaves, and since the cotyledons have become detached the sooner the xylem can be differentiated in the water-absorbing tissues the better.

The lignification of the epicotyledonary xylem usually reaches the cotyledonary node while the seedling is young and prior to the detachment of the cotyledons.

There is also another point in connection with the possible utility of the cotyledonary strands, which being disconnected from the cotyledons and endosperm seem likely to be in the way of any extra development of the epicotyledonary strands. The epicotyledonary traces remain separated from those of the cotyledons for a long time, but in D. Thwaitesii and probably in many others they become connected by the cambial products formed between the separate bundles. By this means the conducting power of the cotyledonary traces is tacked on to those of the epicotyledonary leaves and used in supplying the latter with the requisite food materials. This is therefore a good example of utilization of otherwise useless or abortive tissues during a phase of great urgency.

VI.—REPRODUCTIVE ORGANS. pp. 67–105.

The production of flowers in Ceylon species of Diospyros is usually associated with that of leaves, and is therefore subject to many variations. In many trees of D. Gardneri, D. Embryopteris, and D. sylvatica the flowers immediately follow the new leaves, and since the latter appear more or less regularly every year, an annual production of flowers

may be said to occur. Often, however, a leaf production may take place without a corresponding one of flowers, this being particularly noticeable in young trees having more than one period of leaf production a year. Again, flowers often appear on old woody twigs independent of leaf production, or recur in the same position year after year, sometimes in the axil of an old persistent leaf, and at other times in the old axil of a fallen leaf. In many trees of D. Ebenum and D. Toposia the majority of the flowers occur in the axils of new leaves, and therefore appear mainly at one time of the year, but such copious productions of flowers are invariably preceded and followed by periods of minor floral activity when the flowers appear without any definite relation to the leaves.

It is therefore obvious that no generalizations can be made beyond stating that the greater part of the flower system usually makes its appearance immediately after a copious production of leaves. The importance of realizing the irregular nature of leaf and flower production is great, and one cannot lay too much stress on the fact that in the forests of Ceylon the species of Diospyros have not one fixed time of the year for flower production. In the Sabaragamuwa districts there is not a month in the year when trees of D. insignis and D. hirsuta are absolutely flowerless, and the fact that trees of the same species growing alongside each other may possess either flower buds, mature flowers, ripe fruits, or no reproductive organs whatever during the same month, is sufficient to allow one to dispute any hypothesis based on the idea of a general seasonal periodicity.

It may be further stated that many Diospyros trees probably remain flowerless for many years at a time, and the appearance of sexual organs cannot be correlated with the prevailing seasons. This was the opinion of Thwaites and Trimen, and most forest officers still firmly believe that the majority of Ceylon Diospyros trees flower but seldom.

There are no records of careful observations made upon particular trees for many years in succession, and though the writer is prepared to admit the probability of the above contention, experience in the forests has led him to believe that the production of flowers in Ceylon Diospyros trees is by no means a rare occurrence. The great size of the trees, the inconspicuous nature of the flowers, and the uninhabitable districts in which many of our species occur, have led most people to believe that flower production is much rarer than it really is. We may, however, safely say that there is much irregularity in flower production, and the phenomenon can only be explained by a study of the individual equation of the plant we are dealing with.

Age of Flowering Trees.—In the absence of precise information on the rates of growth of tropical trees we can best state our ideas under this heading in terms of cauline dimensions. The majority of our dry zone species, particularly D. Embryopteris and D. ovalifolia, do not flower until the trees have attained considerable dimensions. Specimens of the former having a circumference of 3 feet and of the latter over 1 foot in girth are now growing at Peradeniya, but have not yet flowered. One specimen of D. quæsita, having a breast-height circumference of 47 cm. (18½ inches) and known to be over sixty years old, has not yet flowered at Peradeniya. Trees of D. Ebenum, D. affinis, and D. Gardneri are known to repeatedly flower at Peradeniya, and have a breast-height circumference varying from 38 to 50 cm. (15 to 19½ inches).

On the other hand, trees of D. hirsuta and D. Thwaitesii in their native habitat flower when their stems have a diameter of 4 to 6 inches ; D. pruriens may flower when the dimensions are still less, and trees of D. acuta and D. attenuata have been seen in flower when the diameter of their stems has not exceeded 25 mm. (1 inch). The following table is given with a view to elicit more precise

information in the future, and the dimensions quoted have been determined personally in the districts mentioned:—

Minimum Dimensions of Flowering Trees.

Name.	Locality.	Breast-height Diameter of Stem in Mm.
D. Embryopteris	Peradeniya	155
D. affinis	Bibile	130
D. oocarpa	Kalugala	180
D. Ebenum	Pindeniya	125
D. montana	Madawachchi	75
D. quæsita	Karawita	250
D. crumenata	Hantane	260
D. Toposia	Gammaduwa	60
D. Gardneri	Hantane	120
D. hirsuta	Ratnapura	65
D. Moonii	Yagirilla	25
D. Thwaitesii	Hewessa	100
D. oppositifolia	Hiniduma	50
D. attenuata	Pasdun korale, near Hiniduma	25
D. sylvatica	Hantane	250
D. acuta	Pasdun korale, near Hiniduma	25
D. Melanoxylon	Bibile	110
D. pruriens	Kadawatta	60
D. insignis	Ratnapura	60
D. ovalifolia	Kanthalai	200

Position of Flowers.—The majority of the flowers, whether solitary or in the form of an inflorescence, appear in the axils of foliage leaves, and are therefore most usually found near the ends of the ultimate twigs. Many species, however, have their flowers disposed on old twigs or branches, this being characteristic for D. Moonii, D. ovalifolia, and D. insignis in particular.

When the flowers are monœcious the females usually appear in the axil of the youngest leaves and the males in the axil of lower leaves. In D. oppositifolia and D. acuta a female flower usually terminates each young shoot; other female flowers occur in the axils of young leaves, but the males occur either in the axil of old leaves, or on woody twigs independent of foliage leaves. The females are thus subject to more exposure, and being exposed to the wind on all sides are more likely to attract insects and to catch wind-borne pollen.

Nature of Flower System.—The nature of the flower system varies with the species and with the sex of the same species. The flowers may be solitary, pedunculate, or sessile, or in the form of an inflorescence having each member supported on a pedicel of varying length. When the peduncle and each lateral pedicel of a cymose inflorescence is very short the flowers form what may be conveniently described as a sessile cluster. The male and female flowers may each form inflorescences; here both inflorescences may be in the form of sessile clusters, as in D. insignis, both inflorescences may have pedicellate flowers, as in D. Embryopteris, or the members of the female inflorescence may be sessile and the males shortly pedicellate, as occasionally occurs in D. Ebenum.

On the other hand, the females may occur solitary and the males as an inflorescence; under this group we may have the female flower and each male flower markedly pedicellate, as in D. quæsita, or both sessile, as in D. Gardneri; we may also have the female sessile, but males pedicellate, as in D. Melanoxylon, or the female pedicellate and the males sessile, as in D. oppositifolia.

Female Flowers.

In fourteen out of our twenty species the female flowers may occur solitary; in nine of these, viz., D. affinis, D. pruriens, D. oppositifolia, D. quæsita, D. sylvatica, D. crumenata, D. Toposia, D. oocarpa, and D. montana, the flower is on a peduncle of varying length, whereas in the remaining five, D. ovalifolia, D. Melanoxylon, D. Gardneri, D. attenuata, and D. Ebenum, the female flowers are sessile.

In the remaining six species the female flowers form an inflorescence which in D. hirsuta, D. insignis, D. Moonii, D. Thwaitesii, and D. acuta is a sessile cluster of three to fifteen flowers; but in D. Embryopteris the inflorescence is a cyme of three flowers, each of which is attached to the short peduncle by means of a short stout pedicel.

It must here be stated that the female flowers of D. acuta, D. sylvatica, and D. Ebenum may occur in the solitary or grouped condition on the same tree. It now remains for us to study the relationships between the parts of a solitary female flower and the members of a female inflorescence.

Development of the Female Flowers in D. Gardneri, D. Embryopteris, and others.—In D. Gardneri the pubescent flower bud arises in the axil of a new or old foliage leaf. The peduncle is very short and rarely exceeds 0·4 cm. in length, but very soon two small leaves appear at right angles to the antero-posterior axis. In addition to these a third leaf may appear between the normal foliage leaf and the anterior side of the flower, and this may be followed by a fourth on the opposite side between the axis and the posterior side of the flower. Under ordinary circumstances, and even if the flowers be cut away so as not to greatly disturb surrounding organs, no development takes place in either of the bracts numbered 1, 2, 3, and 4. If, however, we now study the development of the female inflorescence in D. Embryopteris, we find exactly the same sequence of events, but in addition a flower bud appears in the axil of each of the small leaves on the primary peduncle (pl. IX., figs. 7–10). Similarly with the female inflorescences of other species. It is further to be noted that when the female inflorescence forms a sessile cluster the appearance of each flower is always preceded by that of the small leaf, and in many of them a considerable amount of abortion occurs.

Often in D. Thwaitesii there is a solitary female flower surrounded at the base by an involucre of bracts, abortion having occurred in the axil of the lower bracts. We may therefore arrange the female flower systems in one series to show that the solitary flower arrangement is probably derived from the cymose inflorescence by abortion in the axil of the lower bracts. This is the most likely course of evolution, since the lateral flowers in the inflorescence of D. Embryopteris often drop before they reach maturity in consequence of the pressure exerted by the quickly growing median flower.

Male Flowers.

In every Ceylon species the male flowers occur in clusters of three or more individuals ; in D. attenuata and D. oppositifolia they may also occur solitary in the axil of the younger leaves. Sometimes the cluster of flowers is inconspicuous, as in D. attenuata, but at other times, particularly with D. sylvatica, D. quæsita, and D. Toposia, a single inflorescence may have a height of 50 mm.

The peduncle or the central flower of an inflorescence arises in the axil of a young leaf, which may be of the normal type or greatly reduced ; similarly with each lateral flower or its pedicel. When the individual flowers of a cluster are sessile there is often a great deal of abortion, and the remaining flowers therefore appear surrounded with very many bracts, so that a rudimentary involucre is formed.

The types of male inflorescences are three in number. In the first class we have the primary peduncle and the pedicel of each lateral flower so small as to be undistinguishable to the naked eye, and the inflorescence may therefore be described as a sessile cluster, as in D. ovalifolia, D. hirsuta, D. Moonii, D. insignis, D. Thwaitesii, D. oppositifolia, D. attenuata, D. acuta, and D. Gardneri. In the second class we have each flower disposed on a very short pedicel from 1 to 5 mm. in length, as in D. oocarpa and D. sylvatica. In the third class we have the remaining nine species, in each of which the flowers are supported on very long pedicels often considerably over 10 mm. in length.

Development of the Male Inflorescence.—It will be better to first detail the developmental phases of an inflorescence of the third type, and no better species can be chosen than D. Embryopteris. In the earliest stages the inflorescence appears as a globular apiculate axillary structure, supported on a short stout peduncle and covered by a varying number (two to five) of regularly arranged bracts. As the inflorescence gradually opens, the first pair of bracts are seen to be opposite or subopposite and disposed one on either side, at

right angles to the antero-posterior axis ; these are the first to drop, and each possesses in its axil a semilunar pedicellate flower. Each lateral flower is in close contact with the median flower, which is always the largest and the oldest (pl. IX., figs. 1–4).

A second pair of bracts is seen in the early stages, arranged one on each side at right angles to the first pair, but at different levels ; each of these likewise possesses a small pedicellate flower in its axil. At a much later stage, some time after the fall of the first two bracts, a fifth bract appears between the median flower and the third lateral flower, and in its axil a shortly pedicellate flower arises.

In point of time the median flower arising in the axil of a foliage leaf is not much in advance of the first pair of lateral flowers. The third flower does not, however, appear for some time, and the interval of time between its appearance and the next flower, with which it forms a subopposite pair, is still more prolonged. The appearance of the fifth lateral flower is considerably delayed, and often it does not appear until the majority of the bracts of the other flowers have dropped. We therefore see that the interval of time between the appearance of successive flowers of the same inflorescence increases gradually, and the flowers do not cease to appear until the oldest individuals have undergone considerable expansion and their subtending bracts have dropped.

We thus obtain finally a definite inflorescence having the terminal flower the oldest, but the youngest flower next to it, the development of each lateral flower being to the median centrifugal, but to one another centripetal. (See pl. IX., fig. 5.)

If we now compare the development of the male inflorescence of any other species, approximately the same phases are passed through. In some species the number of lateral flowers is small, as in D. pruriens, whereas other species, notably D. Toposia and D. sylvatica, have a much more complicated system of flowers, in consequence of each lateral

pedicel becoming the main peduncle of another cyme. (See pl. X., figs. 7–8.)

It is obvious from the descriptions given that the inflorescences of the male and female are similar in their phases of development, the only difference being one of degree, since the female more often than not consists of a single flower having a pair of bracts at right angles to the antero-posterior axis, or with two to four bracts along its peduncle. The solitary female flower with its concomitant structures is an exact representation of the early stages of the complex inflorescence of the male. It is quite probable that the whole of the Ceylon species of Diospyros can be traced back to a type of reproductive organs in which the flowers of an inflorescence were numerous and hermaphrodite.

Variation.—Though the solitary flower or inflorescence is fairly constant for the sex of the species, it is not by any means strictly so. The female flower, though occurring solitary in the majority of our species, is liable to be replaced by a simple dichasial cyme. This is particularly frequent in D. acuta, D. sylvatica, and D. Ebenum, and it is probably only a question of further observation to establish the same tendency on the part of the female flower in other species.

The variation on the male side is much more conspicuous. In D. oppositifolia, for instance, instead of a male inflorescence of many flowers, there may be a solitary male flower; in D. Toposia we may observe every variation from a single flower to a complex inflorescence of eighteen flowers.

This variation on the male side is not of any serious consequence to the plant, since the number of male flowers is always greatly in excess of the female. On an average there are about six times as many male flowers as female flowers in monœcious species, and probably a still greater proportion of males in those species which are not monœcious; hence, in the general characters of the inflorescence and individual flowers there is considerably more variation on the male than on the female side.

Sex.

According to Hiern the genus Diospyros is characterized by diœcious flowers, and only rarely is a polygamous or monœcious state to be observed. It is further stated that when such departures from the diœcious condition do occur they do so only casually, and one is left to infer that the variation is one to be explained on individual grounds and is not of specific importance.

Including species imperfectly known, Hiern describes 170, and of these only 7 per cent. are recorded by himself or others as showing a departure from the diœcious condition.

Accordingly, Hiern formed a classification for the whole of the Ebenaceæ, showing the genus Royena, L., with hermaphrodite or rarely subdiœcious flowers and the remaining genera, viz., Euclea, *Linn.*, Maba, *Forst.*, Diospyros, *L.*, and Tetraclis, *gen. nov.*, with diœcious or rarely polygamous flowers.

Confining ourselves to the Ceylon representatives of Diospyros, we find that Thwaites and Trimen believed the genus to be characterized by diœcious flowers, and that the flowers were only very rarely monœcious. Thwaites noted the departure from the diœcious condition in two of our species, and stated that in D. acuta the flowers were sometimes monœcious, and that in D. hirsuta the female flowers are sometimes intermixed with the male.

The main source of error has probably been in that the material at hand has not been very abundant, or the examination has been made upon herbarium specimens or material which had been collected some time previously. In the so-called "male" flowers of D. Gardneri there is very little external character indicative of a fertile pistil in the fresh material, and it is only by continued observation that ripe fruits may be seen.

Herbarium specimens of known hermaphrodite and polygamous flowers of D. affinis, D. hirsuta, and others do not show any prominent external differences from known male

flowers of the same species, and it is only by actual observation of fresh material in the forest that the true sex has been determined. It has been the common experience of myself and many others to regard trees of D. sylvatica and D. Gardneri as males, until they have been felled, when in addition to flowers possessing fertile stamens, abundance of ripe fruits have been obtained on the same branch. In order to further emphasize this condition I may say that the whole of the anatomy and development of seedlings of D. sylvatica, to be published elsewhere, was first worked out from seeds obtained from a tree which has for many years been labelled as a "male," and from which material for sketching the "male" inflorescence has been derived.

From the following notes it will be seen that examination of fresh material in the forest has shown that there is a departure from the diœcious condition in ten out of our twenty species. Speaking generally, the sex appears to be very unstable, the diœcious, monœcious, polygamous, and hermaphrodite conditions having been found. The occurrence of hermaphrodite flowers resulting in a polygamous condition is so frequent that there is every reason to doubt their non-existence in any of the Ceylon species, providing sufficient material can be examined outside the herbarium.

It may be further stated that specimens of D. Thwaitesii have been repeatedly examined, which suggested that the sex of the flower might vary from time to time; this has been described for other plants.* Certain it is that the sex of the flower often exhibits every variation in the same inflorescence of D. sylvatica, and the many stages observed readily allow one to form a series having staminate flowers at one end and hermaphrodite at the other.

The types of flowers characteristic for the different Ceylon species may now be described under the following headings: (*a*) diœcious only, (*b*) monœcious only, (*c*) diœcious and polygamous, and (*d*) diœcious, monœcious, and polygamous.

* Willis, Gynodiœcism, &c. (3rd paper); Proc. Camb. Phil. Soc., 1893.

Diœcious only.—This condition prevails in D. Toposia, D. quæsita, D. pruriens, D. crumenata, D. ovalifolia, D. Melanoxylon, D. attenuata, D. montana, D. Moonii, and D. oocarpa.

In these species the female flowers may be solitary or form a simple or complex dichasium, having the staminodes of each flower with barren anthers. The males may form a cymose inflorescence, sessile or otherwise, in each flower of which the pistil is absent, rudimentary or represented by a bunch of hairs. It is highly probable that if more fresh material is examined at least the polygamous and very possible the monœcious condition will be observed. In many of the species included under this head the male flowers are always very numerous, often as many as fifteen to each inflorescence, and hence the possibility of variation and occurrence of polygamy. In some of the species, notably D. quæsita and D. Toposia, the rudimentary pistil of many male flowers is often of conspicuous size, and a transverse section reveals the presence of irregularly outlined cavities. Further, it is not unlikely that if the staminodes of the female flowers be examined fresh they will yield pollen grains. Very little material has been examined microscopically from this point of view.

The number of members in the staminal whorl and their orientation in the male and female flowers of the same species is sometimes widely different; for instance, in D. quæsita the female flower possesses five staminodes which alternate with the corolla lobes, whereas in the male flowers an indefinite number of stamens occur clustered together in the centre of the flower, and have no individual orientation to one another or to the members of other whorls. Similarly, great differences exist in the staminal whorl of D. pruriens.

In D. Melanoxylon the staminal whorl is very unstable in both sexes, there being ten, sixteen, or twenty stamens in the male, sometimes with the filaments free, at other times united in pairs, and twelve or more staminodes in the female flower having no fixed orientation to the four- to seven-lobed accessory whorls.

Monœcious only.—This occurs in D. oppositifolia and D. acuta.

In D. oppositifolia the female flower is usually solitary and at the end of a young twig. Occasionally a female flower occurs lower down in the axil of old or young leaves. When the flower terminates the young shoot it is usually on a peduncle from 5 to 20 mm. long; when in the axil of a leaf it is invariably sessile and mixed with male flowers. The staminodes are usually four in number, alternating with the corolla segments; or exceptionally eight in number, opposite and alternate with the corolla segments. In every case examined the anthers of the staminodes were barren. The male flowers occur in sessile or subsessile inflorescences in cf. post p. 84 the axil of old leaves or on old twigs. Each flower possesses eight stamens and a rudimentary apical mass of long unicellular hairs in the position of the pistil of other flowers. The stamens are usually paired, the pairs usually alternating with the corolla segments. The resemblance between the orientation of the staminal whorl of the female flower and that of the stamens of the male flower is here very great, and as far as this whorl is concerned we may speak of the flowers as male or female, according to the fertile or barren condition of the anthers.

D. acuta, according to Thwaites, is occasionally monœcious; personally I have never been able to obtain any other condition, though I found it in abundance at Wewella, Weerakanda, Hewessa, and Pasdun korale. The male and female flowers occur in clusters in the axil of old or young leaves, the individuals of the same cluster being of the same sex. As in D. oppositifolia, the female flowers occur mainly in the cf. post p. 84 axil of the younger leaves, the male flowers being below. In the number and orientation of the members of the staminal whorl there is a tendency to variability on the male side. In the male flowers there may be five, seven, or nine epipetalous stamens, usually separate but occasionally united in pairs, and when the latter condition obtains the inner

stamen of a pair is very small and contains very little, if any, pollen when mature.

On the other hand, the staminodes of each female flower are always five in number, epipetalous, and arranged so as to alternate with the corolla segments.

It is therefore to be noted that in the species which are monœcious only the staminodes are constant in position and number, the stamens may equal or double the staminodes in number, and a rudimentary pistil usually occurs in the centre of each male flower. As to whether the male flower can be derived from the female, or *vice versâ*, by sterilization of sporogenous tissue, nothing need be said in this part of the paper.

Diœcious and Polygamous.—This occurs in D. sylvatica, D. Gardneri, D. affinis, D. Embryopteris, and D. insignis.

Under this section we must differentiate between the polygamous condition due to replacement of a staminode by a stamen, as in D. Embryopteris, and that due to the pistil of a male flower exerting its potentiality, as in D. affinis, D. sylvatica, and D. Gardneri.

In D. Embryopteris we have the distinct male and female forms, and the species can be said to be diœcious. The female flowers have four staminodes* alternating with the corolla lobes and a central pistil having an eight-celled ovary. The male flowers have an indefinite number of stamens and a rudimentary pistil. It has, however, been noted by Hiern that the staminodes of the female flower may be replaced by perfect stamens, thus giving rise to a polygamous state. The male flowers of the same species likewise show an occasional fertile pistil, resulting in a polygamous condition on the same tree.

In D. sylvatica, D. Gardneri, D. insignis, and D. affinis we have the diœcious and polygamous conditions well

* Hiern states (p. 258) that D. Embryopteris has one to twelve staminodes in the female flower.

demonstrated. The conditions are the same for each of these species, and a description of one will therefore be sufficient.

Selecting D. sylvatica, we find that in this species we have three kinds of trees, viz., (*a*) female trees, (*b*) male trees, and (*c*) polygamous trees.

The female trees have their flowers arranged either solitary or in simple cymes, each component having four or eight staminodes and a six- to eight-celled ovary. The calyx is usually accrescent and larger than that of the male.

The male trees have dense cymes, each often with fifteen flowers. Each male flower possesses an indefinite number of stamens and thin calyx segments.

The polygamous trees have the flowers arranged as in a male cyme, and among them three types of flowers can be distinguished. In the first section we have hermaphrodite flowers, each of which is characterized by large accessory whorls, twenty-two stamens, and a fertile pistil. The fruits from these flowers possess seeds which in the characters of the testa and embryo exactly agree with those from known female trees. In the second class we have flowers with large accessory whorls, twenty-two stamens, and an abortive pistil showing an ovary one- to six-celled. These never yield good fruits. In the third class we have flowers with small accessory whorls, twenty-two stamens, and an abortive pistil.

It is therefore clear that in the polygamous trees we can obtain every stage from purely staminate to hermaphrodite flowers.

It must not be supposed that the polygamous condition may occur on any tree. There are male trees which never produce anything but staminate flowers and female trees which never possess stamens, and these must be clearly distinguished from those trees showing the polygamous condition.

The difference between the indefinite staminal whorl of the male and polygamous flowers and that of the true female

is very great, and though it is easy to connect the flowers of the third class in the polygamous group with those of the true male, it is not so easy to connect the hermaphrodite flowers of the polygamous group with the ordinary female flowers.

We have again to realize that in the same species there is a wide variation in the number and orientation of the floral parts of male and female flowers.

Diœcious, Monœcious, and Polygamous.—This may occur in flowers of D. hirsuta, D. Thwaitesii, and D. Ebenum.

In these species a very complicated sex relationship exists. If we take as our example D. Thwaitesii, we find that three types of trees exist.

In the first place there are pure female trees. Here the flowers may occur solitary or in small sessile axillary clusters of two to seven flowers, each component having five staminodes disposed so as to alternate with the five lobes of the corolla and a four-celled ovary.

In the second class there are pure male trees having the flowers in axillary groups of four to fifteen. Each flower has ten stamens arranged in five pairs alternating with the corolla lobes, or several pairs and the remainder single, arranged irregularly or as five series. In these flowers the pistil is always rudimentary, and consists of nothing more than a central mass of brown hairs. It is in the third class of trees that complicated relations exist. In this class we have the true male and true female flowers occurring on the same tree, sometimes in separate axillary groups of the same branch, and at other times in the same axillary group. Thwaites noted that in D. hirsuta the female flowers were sometimes mixed with the male. We may therefore speak of the monœcious condition in these species. But in addition to the monœcious condition we may have on the same tree a truly polygamous group or groups of flowers exactly analogous to the polygamous flowers described for D. Gardneri, D. sylvatica, and others. The polygamous

condition is where each flower has ten or more stamens, each with a perfect anther and occasionally a central pistil which ripens into fruit.

It is obvious that a distinct correlation can be established in the number and position of the members of the flowers borne on trees of this class, and since the occurrence is so irregular and the stages established include the male, hermaphrodite, and female conditions, some light may be thrown on the evolution of sex in this genus.

In considering the relations between the members of the flowers on trees of the third class we may at once eliminate the calyx and corolla, since in all the flowers the variation is only one of size, the maximum and minimum dimensions being in the female and male flowers respectively.

The staminal whorl in the male flowers, whether these form a separate cluster or part of a monœcious or polygamous group, consists usually of ten stamens arranged as five pairs, alternating with the corolla segments. In some male flowers there may be only eight stamens arranged as three pairs and two separate individuals, and in others I have met with an irregular epipetalous group of stamens. In the female flowers, no matter where they occur, the staminal whorl is represented by five epipetalous staminodes disposed so as to be alternate with the corolla lobes. The position of the members of the staminal whorl in male and female flowers is approximately the same, and the five single staminodes of the female can be connected with the five groups of stamens usually existing in the male flowers. Since the staminode is really a stamen having a barren anther, we therefore see that the difference between the male and female flowers can be easily accounted for, assuming there has been abortion of sporogenous tissue.

In the gynœcium the number of loculi in the ovary and the number and position of the ovules and seeds is the same, whether the pistil is part of a hermaphrodite or female flower.

It is therefore possible to make a complete series from flowers on the same tree, having staminate flowers at one end, passing through hermaphrodite to female flowers.

In other trees of the same species the sex is either male or female and is fixed.

D. Ebenum is included under this heading, and though the diœcious condition is the most common form for this species, yet observation of fresh material in the forest has revealed the frequent occurrence of the monœcious and polygamous state. The monœcious state consists of female flowers often ripening into good fruit on a pedicel in a male inflorescene. The monœcious condition in D. Ebenum is unlike that in D. oppositifolia or D. acuta, since the female flowers do not occur solitary but as sporadic members of a male cyme. On first examining such a monœcious inflorescence the thought uppermost in my mind was that here we were dealing with a male inflorescence, some members of which had reverted to the condition of a potential gynæcium, but this idea was abandoned in consequence of the fact that each of the female flowers when thus occurring possessed eight staminodes each with a barren anther, and an eight-celled ovary. We therefore have true female flowers occurring in the same cluster as the males.

The female flowers may occur in any part of the inflorescence, but the most usual position is that terminating the inflorescence and therefore occupying the central position. Since the central flower is the first formed we therefore obtain a time relation in the production of sex, the female flowers being produced first and the male flowers afterwards.

The production of female flowers in the axil of the youngest leaves, and that of the males in the older leaves in D. acuta and D. oppositifolia is a sequence to be correlated with this.

In consequence of the complex relationships in species described it is well to realize that the monœcious state in

D. Ebenum is due to the interpolation of a female flower in a male cyme. The female flower when thus occurring presents no differences from the female flower of diœcious trees, except in that it is pedicellate. In no case have I met with the monœcious form due to the replacement of a female flower by a male.

The occurrence of true male and female flowers in the same inflorescence is of importance, since the characters of the accessory and essential whorls in the male and female are often so widely different. It has been suggested by many observers that since the flowers, the habit, and foliage of what are regarded as the male and female trees of the same species often show great differences, we might be erroneously considering male and female trees of what are really separate species as being of the same species. Subsequent observations demonstrated the frequent occurrence of polygamy, and for a time these gave support to the above contention. Now, however, we have seen that the true male and true female flowers possessing different types of accessory and essential whorls can occur in the same inflorescence, and we can therefore adhere to the former ideas as to the true diœcious form of some species.

Characters of Accessory and Essential Whorls.

Calyx.—The calyx is always inferior and gamosepalous; sometimes glabrous or nearly so, as in D. sylvatica, at other times densely pubescent, as in D. Embryopteris and D. pruriens.

In the male flowers the calyx segments are relatively small and accrescent, whereas in the female and hermaphrodite flowers they attain considerable dimensions and the segments project outwards.

In the Ceylon species the calyx segments are usually very distinct, varying in number from two to seven; the common number of segments is four or five. In some species, however, the calyx segments cannot be distinguished, as in D.

oocarpa ; in D. Toposia the calyx of the male flower is closed in the bud, and bursts irregularly into two or more segments when the flower opens. The calyx segments are most strongly marked in D. Embryopteris, D. Ebenum, D. Gardneri, &c., but in many of the species belonging to this class the conspicuousness of the calyx segments becomes reduced during the development of the fruit.

The calyces of the female and hermaphrodite flowers can be divided into several classes, the first comprising those which even after fruiting remain small, thin, and horizontal, as in D. pruriens, D. montana, D. sylvatica, D. attenuata, D. oocarpa, and others, the second class comprising those which, though they have undergone considerable enlargement during the formation of the fruit, remain relatively thin and horizontal, as in D. Moonii and D. hirsuta, the third those which increase considerably in size and form a shallow or deep cup in which the ripe fruit is lodged, as in D. Gardneri, D. oppositifolia, D. affinis, D. quæsita, D. insignis, and many others.

During the formation of the fruit the calyces of the third class show different courses of development. The most usual is to form a very large intersegmental pouch and pointed apices, together with a feeble reflex margin ; this is best seen in D. quæsita ; in other species, notably D. Ebenum, the apices become strongly pointed and horizontal and the margin strongly reflexed ; in D. insignis and D. crumenata the enlarged woody calyx becomes strongly four-sided in consequence of the dying back of the apices of the segments and the very reflex nature of their margins.

Many of the calyces, though highly pubescent in the flower stage, become glabrous in the fruiting stage. The hairs, with one exception, are long unicellular outgrowths from single cells. In D. Ebenum, however, the base of the shallow calyx cup is covered with unicellular and pedicellate hairs, the latter having very much the appearance of globular multicellular glands supported on pedicels of

varying length. I have not met with these multicellular glands on the calyx of any other species, though they occur abundantly over the carpellary wall of D. Embryopteris (pl. XIX., figs. 10–11).

The calyx usually persists on the ripe fruits, but in many of those which form deep cups the fruits seem to become detached and the calyx is left on the twig.

The general characters of the calyx segments and the ferrugineous hairs with which they are very often coloured are, according to Hallier,* of systematic importance and comparable to similar structures in the Pittosporaceæ.

The same botanist† also calls attention to the fact that in Scytopetalum the segments of the small calyx cannot be distinguished, and suggests an affinity with the Ebenaceæ. We have seen that in D. oocarpa particularly, and also to a less marked extent in D. Toposia, the calyx segments are often undistinguishable.

Corolla.—The segments are united and usually, though by no means always, isomerous with those of the calyx. The colour is yellow, white, or greenish. The tube and segments are often covered with silky or brown hairs, sometimes on the outside only, at other times on both sides. The margin of the segments in species like D. hirsuta is very hairy. The segments are usually equal, and according to Hiern‡ are contorted sinistrorsely in æstivation as regarded from inside, except D. oocarpa, in which the æstivation is variously imbricated. The corolla is occasionally very conspicuous, as in D. Embryopteris and D. Ebenum, but most usually is small and unattractive, as in D. Toposia and D. attenuata. The segments may be relatively long, as in D. pruriens, or very short as in D. Toposia.

For convenience we will distinguish two types of corolla. The first type comprises all those in which the corolla

* Hallier, *l.c.*, p. 33. † Hallier, *l.c.*, p. 36. ‡ Hiern, *l.c.*, p. 60.

is widely open, as in D. Embryopteris and the urceolate flowers of D. sylvatica, the second all those in which the corolla tube communicates with the exterior by a very small aperture. The majority of the species have the corolla of male and female flowers of this type, and in many of them the aperture is exceedingly narrow and appears to be closed until a late stage in the development of the flower. The smallest apertures are to be seen in D. attenuata, D. quæsita, and D. Toposia.

The smallness of the aperture renders it impossible for any but the smallest insects to enter them, and this, together with the inconspicuous nature of the flowers in general, may yet be found to be correlated with the evolution of sex in this genus.

The sympetalous corolla with imbricated æstivation reminds one of the Styraceæ, Sapotaceæ, and Ilicineæ*. It is also true that the corolla segments are often deeply partitioned, and that such bear a resemblance to polypetalous orders.

Hallier† lays stress upon the fact that the corolla segments are alternate with the five small, narrow and acuminate calyx segments in Pittosporaceæ and the Ebenales. This cannot be seriously regarded as of great importance, though one cannot but admit that the accessory whorls of, say, Pittosporum Timorense, *Bl.*, have a strong resemblance in form, colour, and texture to those of the male flowers of Diospyros species.

Staminal Whorl.—The staminal whorl is in the form of an epipetalous, hypogynous, or perigynous ring of stamens or staminodes in the male and female flowers respectively; it is present in the flowers of every Ceylon species of Diospyros, and as an essential whorl is characteristic of the genus throughout the world.

The components of the staminal whorl have a much more constant orientation and number in the female than in the

* Hiern, *l.c.*, p. 62. † Hallier, *l.c.*, p. 33.

male flowers, and it is not always easy to correlate the members in the different sexes of the same species. The relation between the male and female staminal whorl is sometimes very simple, as in D. hirsuta, where there are five staminal organs in each male and female flower disposed so as to alternate with the corolla lobes. In the majority of Ceylon species, however, the staminodes of the female flowers are much fewer than the stamens in the male, a typical instance of which is seen in D. sylvatica, the male flowers of which have from thirteen to twenty stamens and the female flowers only four staminodes. The staminal whorl is of great interest, and since we have for the first time a complete collection of male and female flowers of every Ceylon species of Diospyros, a detailed account is here given.

The Staminal Whorl of the Male Flowers.—In every species of Ceylon Diospyros the male flower possesses many perfect stamens. These occur either as an epipetalous ring having a definite or indefinite orientation to the accessory whorls, or as a central hypogynous group; sometimes both conditions are observed in the same flower.

The filament is white or yellow and varies in length from 0·25 to 0·35 mm.; it is perfectly glabrous in some species, *e.g.*, D. acuta and D. affinis, and densely pubescent in others, *e.g.*, D. oppositifolia and D. Embryopteris.

The anther is usually brown in colour and when mature measures from 0·2 to 0·3 mm. in length; sometimes it is strongly apiculate in consequence of the presence of a large number of unicellular hairs which seem to have a duty to perform in the dissemination of pollen; at other times it is perfectly glabrous. Each anther is lanceolate-linear in shape, erect, two-celled, and dehisces by two longitudinal slits.

It is characteristic of the stamens in the majority of the male flowers to exhibit fusion; sometimes the filaments are united throughout their lengths, at other times only for a short distance. In the case of D. hirsuta there are five separate stamens alternating with the corolla lobes; in D.

Gardneri the numerous stamens are arranged in pairs, the inner stamen of each pair having a shorter filament united throughout to the filament of the outer stamen; in D. Ebenum the stamens are united to form groups of three or four, the filament of the individuals of each group being united in the basal part, and therefore attached to the corolla as a single column; in D. pruriens the fusion has gone to such an extent that a single column formed by the fusion of the filaments of twelve or more stamens exists, similar to what occurs in the Malvaceæ. The importance of these stages in the fusion of the stamens when numerous will be discussed later.

We will now describe the types of male staminal whorls met with in Ceylon species.

(*a*) The simplest type is that in which the stamens are few in number and disposed so as to be in definite orientation to the members of other whorls. This is seen in D. hirsuta and D. Moonii, where each male flower possesses five epipetalous stamens alternating with the corolla lobes.

(*b*) A slightly more complex type is where the number of stamens is in excess of the members of any other whorl and their orientation becomes variable. In D. oppositifolia there are eight stamens usually arranged as four pairs alternating with the four corolla lobes. The members of each pair are separate from one another throughout their length, and a variation occurs when the members of one or more pairs become relatively widely separated. In D. acuta there may be only five stamens alternating with the corolla lobes, or there may be seven or nine, in which case some of the number may be single and the remainder as pairs with fused filaments. In D. Gardneri the complexity is increased, since there may be from six to eight pairs of stamens definitely orientated to the corolla lobes, or a monadelphous ring of stamens may occur.

(*c*) The next type is where the number of stamens is very large and no orientation to other whorls can be distinguished. In D. Embryopteris the male flower may possess from

twenty to forty stamens arranged to form an epipetalous ring, a hypogynous group, or part epipetalous and the remainder hypogynous. The stamens are nearly equal in length and occasionally the filaments are fused at the base. In D. Toposia there are from eighteen to thirty-four stamens of unequal length usually forming a hypogynous central group. In D. Melanoxylon there may be from ten to twenty stamens usually paired and forming a hypogynous group terminating the receptacle. In one flower there were thirteen stamens arranged as five pairs, each having the inner stamen shorter than the outer one, one pair with individuals of equal length, and one long stamen separate from all others.

In another flower of the same species there were fifteen stamens arranged in two whorls, the outer with eight and the inner with seven members. In the outer whorl four were arranged as two adjacent pairs and the remaining four as separate successive stamens; the inner whorl consisted of two united at the filament and the remaining seven separate.

In all those cases where there is an outer and inner whorl the stamens of the inner whorl are always shorter than those of the outer, the difference in length being usually in the filament.

In the male flowers of D. Ebenum similar variations may be noted in the number and position of the stamens. The number varies from about sixteen to thirty-five, but in the majority of flowers examined they are arranged as eight groups, each group having two, three, or four anthers supported on filaments of varying length. These eight groups are usually epipetalous and arranged opposite to and alternate with the corolla lobes. If we take one group of four stamens, we find it to be composed of a basal pedicel 0·1 cm. long, and bearing at this level two lateral, fertile, sessile anthers; above this level a third anther disposed introrsely is given off, and on the continued filament above this level is the fourth anther, always the outermost and disposed introrsely. The total length of such a staminal

group is often over 5 mm. In one flower there were six groups each with four stamens ; and two groups each with two.

(*d*) In the last class we may include all those species the male flowers of which have numerous stamens united to form a central hypogynous column. This is typified in the staminal whorl of D. pruriens. According to Hiern* the stamens are thirteen or fourteen in number and always connate at the base and surround the hairy rudiment of the ovary. In examining fresh material in the forest the stamens of the male flowers were seen to form a central column, the filaments being completely united at the base. Towards the base seven separate stamens could be distinguished, each of which consisted of a short white curved filament and an anther disposed introrsely ; projecting above this outer ring is a yellowish white stout pedicel 3 mm. in length which terminates in five sessile introrse anthers, the pedicel presumably being composed of the united filaments belonging to the five stamens. The total length of this staminal system is 6 mm., and its members exhibit no great variations except in that one may be epipetalous. I have not been able to determine the same condition in the scanty herbarium material of D. pruriens.

It is obvious that in the staminal whorl of the male flowers there are very many characters which can be used in the study of the ontogeny and phylogeny of the genus Diospyros. In descriptions of many species the staminal whorl is not even mentioned, and a somewhat detailed description will therefore be given in this work.

In the regular orientation of a fixed number of stamens, as in D. acuta and D. oppositifolia, and in the paired arrangement of the stamens, as in D. Gardneri, there is a strong resemblance to the Sapotaceæ. Further, the occurrence of a fixed number of stamens and staminodes in the male and female flowers of species which can assume the hermaph-

* Hiern, *l.c.*, p. 43.

rodite and monœcious condition is suggestive of the genus Sideroxylon and others, where stamens and staminodes are known to occur in the same flower.

In the indefinite groups of stamens a resemblance to Styraceæ and many polypetalous orders, particularly with the Anonaceæ and Ternstrœmiaceæ is suggested.

On the other hand, the central column of united stamens (D. pruriens) and the extensive union of filaments in other species is suggestive of like features in the Malvaceæ and Geraniaceæ, and Hallier asserts,* though without giving good reasons, that the Ebenales have their origin closely connected with the Malvales, Geraniales, and Theales. That botanist also states† that the genus Scytopetalum, in that it shows numerous stamens inserted on the base of the corolla and on the flat axis of the flower, and in the arrangement of the anther when in bud, possesses characters which bring it near to the Ebenales.

It is important to realize that in the staminal whorl of the male flowers of only twenty species there are types of character which are only met with in natural orders now widely separated.

The Staminal Whorl of the Female Flowers.—The members of this whorl in the female flowers are but slightly known. They occur nearly always as an epipetalous series, and only rarely, as in occasional flowers of D. Toposia and others, in the hypogynous position.

The filament is very similar in colour, form, and dimensions to that in the male flower.

The anther is usually hastate in form, and is regarded universally as barren. It consists, as seen in transverse section, of regularly disposed parenchyma with a small strand of vascular tissue in the centre.

The filament is usually glabrous, but the anther in some species, notably D. hirsuta and D. Thwaitesii, is strongly apiculate in consequence of the presence of numerous long

* Hallier, *l.c.*, p. 85.

† Hallier, *l.c.*, p. 36.

unicellular hairs, as in the anthers of perfect stamens from the male flowers.

In point of number the staminodes are, compared to the stamens of the male, very few. Usually the number is the same as that of the corolla or calyx segments. The series alternate with the corolla lobes when the number of members of both these whorls is the same, as in the four staminodes of D. oppositifolia, D. sylvatica, and D. Embryopteris, and the five staminodes in D. acuta, D. Thwaitesii, and D. hirsuta.

When the staminodes are an exact multiple of the corolla segments they are disposed opposite to and alternate with them, as in the twelve staminodes of D. Melanoxylon, and the eight staminodes of D. Gardneri and D. Ebenum. When the number of the calyx and corolla segments varies the number of staminodes usually shows exactly the same numerical variations, as in D. insignis, D. attenuata, and D. affinis, where the flowers may have their parts in fours and fives, and even threes.

In D. Toposia there seems to be an erratic number of twelve to sixteen staminodes arranged either epipetalous or hypogynous.

Pistil.—The pistil is represented in the male flowers of polygamous trees by a central, hairy, apiculate, or flattened disc ; in female flowers it is sub-globose or ovoid in shape, green, and glabrous or hairy ; in D. Embryopteris and D. pruriens the carpellary wall is covered with a dense layer of multi- and uni-cellular hairs which persist in the fruit ; the stigmas are green and sessile ; the ovary is four-, eight-, or ten-celled ; the ovules are pendulous from the top of each cell of the ovary.

The relation of the Staminal Whorl in Male and Female Flowers.—A staminode is similar in form and size to a stamen, and differs from it mainly in that its anther is barren. It may be possible to derive one from the other, and with this object in view I have drawn up a table showing the number and orientation of the members of the staminal whorls for each species.

Group A.—Species which may be Diœcious, Monœcious, and Polygamous.

Abbreviations: c.s. = corolla segments; epi. = epipetalous; alt. = alternate; opp. = opposite; hyp. = hypogynous.

	Stamens of Male Flower.		Staminodes of Female Flower.	
	No.	Arrangement.	No.	Arrangement.
D. hirsuta	5	epi.; alt. with c.s.	5	epi.; alt. with c.s.
D. Thwaitesii	10 or variable	epi.; paired and alt. with c.s. as 5 series; or irregular	5	do.
D. Ebenum	16, 20, 32	epi.; connate groups to form series of 8 alt. and opp. to c.s.	8	epi.; alt. and opp. c.s.

Remarks.—Exact equality in number and position in one species; in each of the others the groups of stamens are equal to the separate staminodes in number and position.

Group B.—Species which are Monœcious only.

	Stamens of Male Flower.		Staminodes of Female Flower.	
	No.	Arrangement.	No.	Arrangement.
D. acuta	5, 7, 9	epi.; separate or paired	5	epi.; alt. with c.s.
D. oppositifolia	8	epi.; four pairs usually alt. with c.s., but variable	4 (rarely 8)	do.

Remarks.—Stamens exact multiple of staminodes, exact equality or slightly variable, not widely different.

Group C.—Species which may be Diœcious or Polygamous.

	Stamens of Male Flower. No.	Stamens of Male Flower. Arrangement.	Staminodes of Female Flower. No.	Staminodes of Female Flower. Arrangement.
D. Gardneri ...	12–16 ...	separate or paired in a series of 8 ...	8 ...	epi. ; alt. and opp. with c.s.
D. sylvatica ...	13–22 ...	epi. ; grouped to form series of 8 or 10	4 ...	epi. ; alt. and opp. with c.s.
D. Embryopteris ...	24, 30, 40, 64 ...	epi. ; grouped irregularly ...	4 ...	epi. ; alt. with c.s.
D. affinis ...	6–16 ...	single or grouped	6–8 ...	epi.
D. insignis ...	14–20 ...	epi. ; single or grouped ...	4–5 ...	do.

Remarks.—Irregular. In some the stamens and staminodes are in equal numbered series, or former in multiple series of latter, or there may be an inconstant number and orientation of stamens and even staminodes.

Group D.—Species which are Diœcious.

	Stamens of Male Flower. No.	Stamens of Male Flower. Arrangement.	Staminodes of Female Flower. No.	Staminodes of Female Flower. Arrangement.
D. attenuata ...	4–6 ...	epi.	4–5 ...	epi.; alt. with c.s.
D. Melanoxylon ...	8, 10, 16, 20 ...	single, or connate to form series of 8...	8, 10, or 12 ...	epi. or hyp.
D. pruriens ...	12–14 ...	hyp.	5 ...	—
D. quæsita ...	16 or x ...	hyp.	5 or x ...	epi.; alt. with c.s.
D. crumenata ...	8–14 ...	hyp. or epi.	8 ...	epi.; alt. and opp. c.s.
D. Toposia ...	18–33 ...	— ...	12–16 ...	epi.
D. ovalifolia ...	13–20 ...	single or grouped	4 or (1–7) ...	—
D. montana ...	16 or x ...	single or united to form a series of 8	4–12 ...	—
D. oocarpa ...	9–14 ...	epi. or hyp.	3 ...	epi.
D. Moonii ...	5 ...	— ...	5 ...	—

Remarks.—Very irregular ; more variable than any of the foregoing groups. In two or three species only is the number of staminodes constant. This group contains half the Ceylon species.

The most perfect agreement in number and position of members of the staminal whorl is in Group A, where the sex relationship is the most complicated, and there is least agreement in Group D, where the sex is diœcious only.

It would appear that the greater the departure from the diœcious condition, the more nearly do the male and female staminal whorls agree; the diœcious condition is further from the hermaphrodite state than any of the Groups A, B, and C.

From the above table we can deduce certain generalizations which will probably throw some light on the exact ontogenetic relationships of the organs considered. The remarks on this subject are made purely in relation to the flowers of the Ceylon species examined, and it is possible that examination of other species in other countries may lead to quite contrary or to similar conclusions.

Since we have classified certain species into groups according to their sex relationships, it will be convenient to adhere to the above plan in describing the staminal whorl in each sex group.

We will commence with Group A, in which there are species having the monœcious, diœcious, and polygamous condition. The complicated sex relationships here existing show that it is possible to have on the same tree every stage between a perfect hermaphrodite flower and a staminate or pistillate flower. The hermaphrodite flower in giving rise to a staminate or pistillate flower must undergo abortion of the gynœcium and anthers respectively. In every pistillate flower an epipetalous ring of staminodes exists, and in every staminate flower a rudimentary pistil remains. Can it be that the unisexual flowers have been derived from the hermaphrodite, or *vice versâ?* In one species of this group, viz., D. hirsuta, we see that in number, form, and orientation cf. p. 89. the stamens of each male flower exactly agree with the staminodes of the female flower. Such equality in the staminal whorl does not occur in any other Ceylon species of Diospyros. The complex sexual relationships may have

been derived from a hermaphrodite type by sterilization without reduction in number of parts.

If the unisexual type was the primitive, the flowers are now perhaps progressing towards the production of an uniform hermaphrodite type. When one considers how definitely monœcious or diœcious many other species are, and that sterilization of sporogenous tissue is frequently met with in the ontogeny and phylogeny of the higher plants, it seems more reasonable to regard the more specialized condition of unisexuality as the latest phase in development, and, in view of other facts, to believe that the hermaphrodite condition is the more primitive in this genus. The female inflorescences in many species appear to have undergone much abortion; this is probably true of the parts of the flower also. It is not meant to imply that the species showing this condition are necessarily members of the most primitive section of Diospyros. The statement is made purely in relation to the evolution of sex in Diospyros, a development which may or may not be correlated with that of the vegetative organs.

It would therefore seem an easy task to derive the present mixed sexual condition in D. hirsuta from a primitive hermaphrodite flower. In the production of female from hermaphrodite flowers the anthers, though persisting, become barren. It seems more reasonable to regard a staminode as being a stage in the abortion of a stamen, rather than one in the development of a stamen towards fertility.

If, however, we consider another species showing the same variation in sex, viz., D. Thwaitesii, the evolution from the hermaphrodite flower is more complicated. In this species the staminodes are, as in the female flowers of D. hirsuta, five in number and arranged on the corolla so as to alternate with their lobes. In the male flowers, however, the number of stamens always exceeds that of the staminodes of the female flower, there being usually ten, and in one case twelve fertile stamens present. It is interesting to note that when there are ten stamens present these are arranged

in pairs, each pair alternating with the corolla segments and being attached to the corolla as one or two filaments.

When there are less than ten stamens some are arranged in pairs and others singly, but always as a series of five alternating with the corolla lobes. It would thus appear that if we have to maintain the importance of abortion we must have the primitive hermaphrodite flower with numerous stamens arranged in pairs or otherwise. It would by no means necessitate a complex series of changes to derive the five-seried staminal whorl of the female flower from that of the male, the barrenness in the anthers of the staminodes being followed by a reduction of each pair to a single member; the inner stamen is always small.

Now, let us take the case of D. Ebenum, the flowers of which may be polygamous, diœcious, or monœcious. We have seen that though the male inflorescence and female flowers usually occur on separate trees, examples have been found where a true female flower replaced a member of a male inflorescence. The staminal whorl of the female flowers is constant in number, form, and orientation. There are always eight epipetalous staminodes alternating with and opposite to the corolla segments. In the male flowers a variable number of stamens occur, but coalescence of the filament occurs so frequently that the resultant number of groups is relatively small. In one case there were sixteen stamens, either single or in groups of two and three, while in another flower thirty-two stamens occurred showing various degrees of coalescence, but in each of these the resultant groups were eight in number and arranged so as to alternate with the corolla segments. Hiern* mentions the occurrence of as many as thirty-two stamens on eight filaments.

This being the case, we have another example in which the origin of unisexuality can be easily understood, since the staminal whorl always forms a series of eight. The monœcious state would represent the intermediate between a

* Hiern, *l.c.*, p. 208.

hermaphrodite and diœcious condition. It is important to realize that here we have a species which is mainly diœcious, but where the staminal whorls of male and female flowers agree in number, if we regard a group in the male as equivalent to one member in the female.

In the species belonging to this group the production of a pistillate flower is attained by sterilization of the male sporogenous tissue (the anther still persisting) followed by a reduction of pairs or groups to single members. The original hermaphrodite flower still occurs on polygamous trees and always possesses stamens of different sizes, the innermost being the smallest.

The accessory whorls of the male and female flowers of this and in fact of all the other species are widely different, but since the differences are those of size and form they may be neglected in considering the evolution of unisexuality in Diospyros.

If we now consider the species in Group B, D. acuta and D. oppositifolia, which are only known in the monœcious condition, we find that they can be easily arranged in a series to show the similarity in the whorls of male and female flowers. In D. oppositifolia the female flowers usually possess four epipetalous staminodes alternating with the corolla segments. In one female flower there were eight separate staminodes arranged so as to be alternate with and opposite to the corolla segments, each being typical in form and possessing a completely barren anther. In the male flowers of this species there are always eight epipetalous stamens usually paired, with the inner member the shorter of the two, but each stamen is attached to the corolla by its own filaments. The pairs invariably alternate with the corolla segments, though this orientation is liable to variation. The variation in the male staminal whorl is where the members of one or more pairs are not exactly opposite one another, a deviation from the normal which tends to simulate the occasional eight separate staminodes of the female flower. It is therefore very easy to correlate the staminal whorl of the male and female flowers of D. oppositifolia with

one another and consequently to derive both from a common sex type.

In D. acuta the staminal whorl of the female flowers consists of five epipetalous members alternating with the corolla segments. The male flowers have, according to Hiern,* from four to five stamens, corresponding to the number of accessory whorl segments, and presumably alternating with those of the corolla. It would thus be quite as easy to derive each sex from a common hermaphrodite flower as with D. oppositifolia.

The male flowers of D. acuta, though usually possessing five epipetalous stamens alternating with the corolla segments, often have seven to nine epipetalous stamens, single or united in pairs and of very unequal length. If the sexes in this species have originated from a common hermaphrodite flower then the original type may have possessed numerous stamens, which in the evolution of the female flower have undergone abortion at a quicker rate than in the male. The very small stamens which occur when the total number is more than five per male flower are perhaps in their last stages, and may represent a phase passed through in the ontogeny of the female staminal whorl from the hermaphrodite type.

We have therefore seen that in considering flowers of species which are (*a*) diœcious, monœcious, and polygamous, and (*b*) monœcious only, the staminal whorls of the male and female flowers are at the present time in general agreement in number, form, and orientation, and the sexes in these species can be derived from a hermaphrodite type of flower having a relatively large number of stamens. In the remaining groups, which are either diœcious only or diœcious and polygamous, the relationships are more complicated.

If we take the Group C, which shows the diœcious and polygamous condition, we find a great variation in the staminal whorl of the different species. The simplest arrangement is perhaps in D. Gardneri. Each female flower

* Hiern, *l.c.*, p. 183.

of this species possesses eight epipetalous staminodes arranged opposite to and alternate with the corolla segments. In the male flowers the number of stamens is large, there being from twelve to sixteen in each flower. When sixteen in number they are usually as eight pairs, the members of each pair being united at the base of the filaments and having the inner stamen smaller than the outer. When only twelve stamens occur these are often arranged as four pairs and four single.

In each case, whether there are sixteen or twelve, they always form an epipetalous series of eight, each pair being either opposite to or alternate with the corolla segments. The inner stamens are always small, and by their abortion a series of eight would result. This condition, which prevails in many flowers, may represent the transition of the staminal whorl of the female flowers, in which case it would be easy to derive both sexes from a common hermaphrodite flower having a large number of stamens. Such a hermaphrodite flower does exist at the present time in those trees showing the polygamous condition. In the hermaphrodite flowers there may be as many as sixteen perfect stamens arranged as a monadelphous hypogynous ring, or arranged part epipetalous at the base of the corolla and part hypogynous. The parts of the pistil and also the seeds of polygamous flowers resemble those of true female flowers. If we assume that the primitive type of flower was hermaphrodite, then a very definite abortion in either of two directions must have taken place, some of the trees having, so to speak, allowed the pistil of every flower to entirely abort, while others reduced the number of stamens in each male flower and eventually suffered sterilization of the male sporogenous tissue. Other trees have undergone occasional sterilization of the pistil, resulting in the polygamous state so prevalent at the present time.

The next most simple case in this group is seen in D. sylvatica. In this species the female flower possesses four epipetalous staminodes disposed so as to alternate with the

corolla segments. The male flowers possess a very large number of stamens, there being rarely less than sixteen and very often over twenty-two in each flower. The stamens are nearly all in pairs, each having the inner stamen shorter than the outer and with the filaments of each pair united throughout the greater part of their length; sometimes three anthers are supported on the same united filament.

In some flowers I have found eight pairs arranged opposite to and alternate with the corolla segments, but in by far the greater number of flowers the pairs of anthers are in excess of twice the corolla segments. In one flower possessing ten pairs of stamens there was always a pair alternating with the corolla segments; the remaining six pairs were arranged as two pairs on each of two corolla segments and a separate pair on each of the other two corolla segments.

If we allow that in the production of the female flower sterilization and reduction in number has occurred, we can easily understand the derivation of the four-seried flower from one having staminal members alternate with and opposite to each corolla segment, as is now seen in male flowers possessing eight groups of stamens. Hence the evolution from the hermaphrodite type is rendered possible.

In D. Embryopteris we have a difficult case, since there is practically nothing to connect the four staminodes of each female whorl with the male ring of thirty or forty stamens. The indefinite stamens in each male flower are sometimes separate, at other times united in pairs, and may be epipetalous or hypogynous. In D. affinis the conditions are almost the same as in D. Embryopteris, since the male staminal whorl consists of sixteen or more members apparently disposed without any definite relation to the accessory whorls. The stamens occur in pairs or are single, and form an epipetalous ring or hypogynous group. Each female flower possesses from six to eight staminodes arranged on the corolla opposite to and alternate with its segments.

Hiern* gives the number of stamens in each male flower of D. affinis as six to sixteen, usually about nine, and some or all in pairs. It is thus clear that in D. Embryopteris and D. affinis the staminal whorls are widely different, and until some intermediate links have been observed the evolution of the sex must remain particularly problematical.

Turning to Group D. (diœcious only), in D. attenuata the members of the staminal whorl are few in number. Each female flower possesses four to five epipetalous staminodes which alternate with the corolla segments; whereas each male flower has a variable number, four to six, of epipetalous stamens, but their orientation is not constant. It is somewhat remarkable if no fixed orientation exists when the members of the male staminal whorl are so few in number. The male flowers are so very small, often less than 1 mm. diameter, that to determine the exact orientation is a difficult undertaking.

The flowers of D. Melanoxylon show a variability in the staminal whorl in both sexes. The female flower possesses accessory whorls in parts of five and six. In those I have examined there has usually been twelve staminodes, either hypogynous or epipetalous, but in positions opposite to and alternate with the corolla lobes. Hiern† states that the staminodes may be eight or ten in number. Each male flower possesses from eight to twelve and even sixteen stamens. When sixteen in number they are always in eight pairs, though according to Hiern‡ it is rare that one finds eight single stamens only. In one flower there were twenty stamens arranged as a hypogynous group. The variability in number of stamens and staminodes and their occurrence mainly in the hypogynous position renders it inadvisable to make any definite statement as to the derivation of one from another or from a common parent.

In the flowers of D. pruriens and D. quæsita the staminodes of each female flower are equal in number to and alternate with the corolla segments, whereas the male flowers possess a more or less hypogynous group of twelve or twenty

* Hiern, *l.c.*, p. 169. ‡ Hiern, *l.c.*, p. 159. † Hiern, *l.c.*, p. 160.

stamens. In D. crumenata the staminodes of each female flower are in number an exact multiple of the corolla segments and are disposed opposite to and alternating with them, whereas the male flower resembles D. quæsita and D. pruriens in the indefinite hypogynous character of the stamens.

There is one species—D. Toposia—in this group which shows an unstable staminal whorl in the female flowers, the number usually being greatly in excess of the members of other whorls, and presents no fixed orientation to them. Each female flower of D. Toposia may possess from twelve to sixteen staminodes, which form an epipetalous or partly hypogynous ring; the stamens of each male flower may be from ten to over thirty in number, of unequal length, forming a hypogynous group terminating the receptacle.

VII.—AFFINITY.

The phylogeny of the Ebenales has formed the subject of much discussion.

Hiern (p. 62) states that the Ebenaceæ shows the closest affinity to the Olacineæ, Styraceæ, Anonaceæ, Ternstrœmiaceæ, Sapotaceæ, and Ilicineæ, but also draws attention to the points of difference between these natural orders and the Ebenaceæ. He also states (p. 63) that other orders including Tiliaceæ, Magnoliaceæ, and the Euphorbiaceæ show affinity in a less degree to the Ebenaceæ.

Miers compares them with the Anonaceæ and suggests their grouping among the polypetalous section; Choisy points out their proximity to the Ternstrœmiaceæ.

Parmentier, in his monograph on the histology and morphology of the Ebenaceæ, does not commit himself to statements as to the phylogeny of the natural order.

Hallier, on the other hand, points out that there are many features in which the Ebenales resemble many other natural orders, and in this respect goes into much more detail than Hiern.

Under the circumstances I cannot do better than point out the main facts as supplemented in the present paper, and

leave the question of affinity until detailed information for the remaining species is at hand.

The fossil species described by Unger, Ettingshausen, Massalongo, and others, the present distribution through tropical regions of the eastern and western hemispheres, in sub-tropical South Africa and Madagascar, and the occurrence in temperate regions are suggestive of great age. The fossil forms, the conspicuous differences between existing species, especially between those in Ceylon, together with the probable early extinction by natural causes of many Ceylon species, suggests the likelihood that the Ebenaceæ had in the past a much wider distribution and a larger number of species than at the present day.

The great point of interest in connection with the Ceylon species is the fact that a good artificial key for working out the species can be constructed on separate characters, *e.g.*, the leaf, flower, or seedlings. The differences in leaf characters are very marked. It is impossible to confuse the tough large leaf of D. Moonii or D. acuta with the thin leaves of D. Thwaitesii and D. montana, or with the thin hairy leaves of D. pruriens. The pellucid character of the veins in leaves of D. Ebenum, D. Embryopteris, D. Toposia, and D. Gardneri separates these species from one another and from all other species, and questions of size and form provide sufficient differences for separating the remaining species. Then again we have seen that it is very convenient to group the species according to their sex characters.*

A good artificial key for the Ceylon representatives can be made on the characters of the seedlings alone, the classification being based on the number of traces per cotyledon, abortion or persistence of the median cotyledonary traces, characters of cotyledons, epicotyledonary leaves, and hypocotyl.

The secondary xylem is the most constant structure throughout the genus, and in the respective species shows differences only in percentage number of the elements.

* Sex in Diospyros, Brit. Assoc., Belfast, 1902. p. 819 (1903).

[*To be continued in next number.*]